# The Distribution of Certain Benthonic Algae in Queen Charlotte Strait, British Columbia, in Relation to Some Environmental Factors

ROBERT F. SCAGEL[1]

IN COMPARISON with the progress in our knowledge of most groups of plants—especially concerning their life histories and distributions—the advances made in marine phycology and marine ecology have been relatively slow. The limited access to living material or to the facilities to maintain the larger marine algae in the living condition for a prolonged period of time, the difficulties of collection—particularly in the subtidal zone—and the lack of any extensive direct economic importance until recent years have all contributed to this slow progress. However, in spite of these difficulties there has been a considerable amount of interest in the marine algae, including a number of studies of their ecology. Although this interest has been fairly widespread in a number of countries, until recently there has been little activity in the field of marine ecology relating to the benthonic algae on the Pacific Coast of North America and nothing of a comprehensive nature has been published for this area. It is an anachronism that this should be so in a region which received such prominence some 50 years ago through the efforts of a pioneer in the field, the late William Albert Setchell (1893, 1917, 1935).

Knowledge of the effect of temperature on the world-wide distribution of plants both horizontally and vertically had developed gradually over a period of many years. However, it was only during the last hundred years that the attention of phycologists was brought to a consideration of the reasons for the observed distributions of the marine algae. The historical development of this trend of thought and investigation has been reviewed by Setchell (1917). Starting over 50 years ago, through a series of papers from 1893 to 1935, Setchell made a noteworthy attempt to explain the world-wide distribution of marine algae, especially of members of the Laminariales on the Pacific Coast of North America, on the basis of latitudinal and seasonal temperature distributions. The physical data available during this early period were limited, but many of the principles set forth by Setchell concerning the distributions of marine algae are as sound now as when they were first proposed. Except for more precise knowledge of the physical and chemical factors of the environment and the distributions of the algae concerned, much of Setchell's ecological work can still be used as a good foundation for further study. Although it was largely a two-dimensional approach to the marine environment, Setchell's work made a significant contribution to the development of marine algal ecology.

Lamouroux (1825, 1826) had suggested the possibility that temperature stratification in the sea might account for the vertical distribution of the marine algae and had considered the effect of tides on intertidal zonations, but this trend to analyze the vertical distribution of the marine algae was not generally taken up in detail until much later. Coleman (1933) was one of the first to emphasize the use of tide levels to account for the vertical distribution of the marine algae in the intertidal zone. In a study in Oregon, on the Pacific Coast of the United States, Doty (1946) has given further evidence for the relationship between the vertical distributions of marine algae and critical tide levels.

A number of lists of marine algae have been published and attempts have been made not only to relate the floras of one area to another, such as that by Okamura (1926, 1932) in the North Pacific, but also to account in a general way for distributions on the basis of ocean currents, such as that by Isaac (1935) in the area around South Africa and by Tokida (1954) in the region of northern Japan. However, there soon followed a decided shift to intertidal studies of regional areas, such as that by Feldmann (1937) in the Mediterranean and Chapman

[1] Department of Biology and Botany, and Institute of Oceanography, University of British Columbia, Vancouver 8, Canada. Manuscript received March 31, 1960.

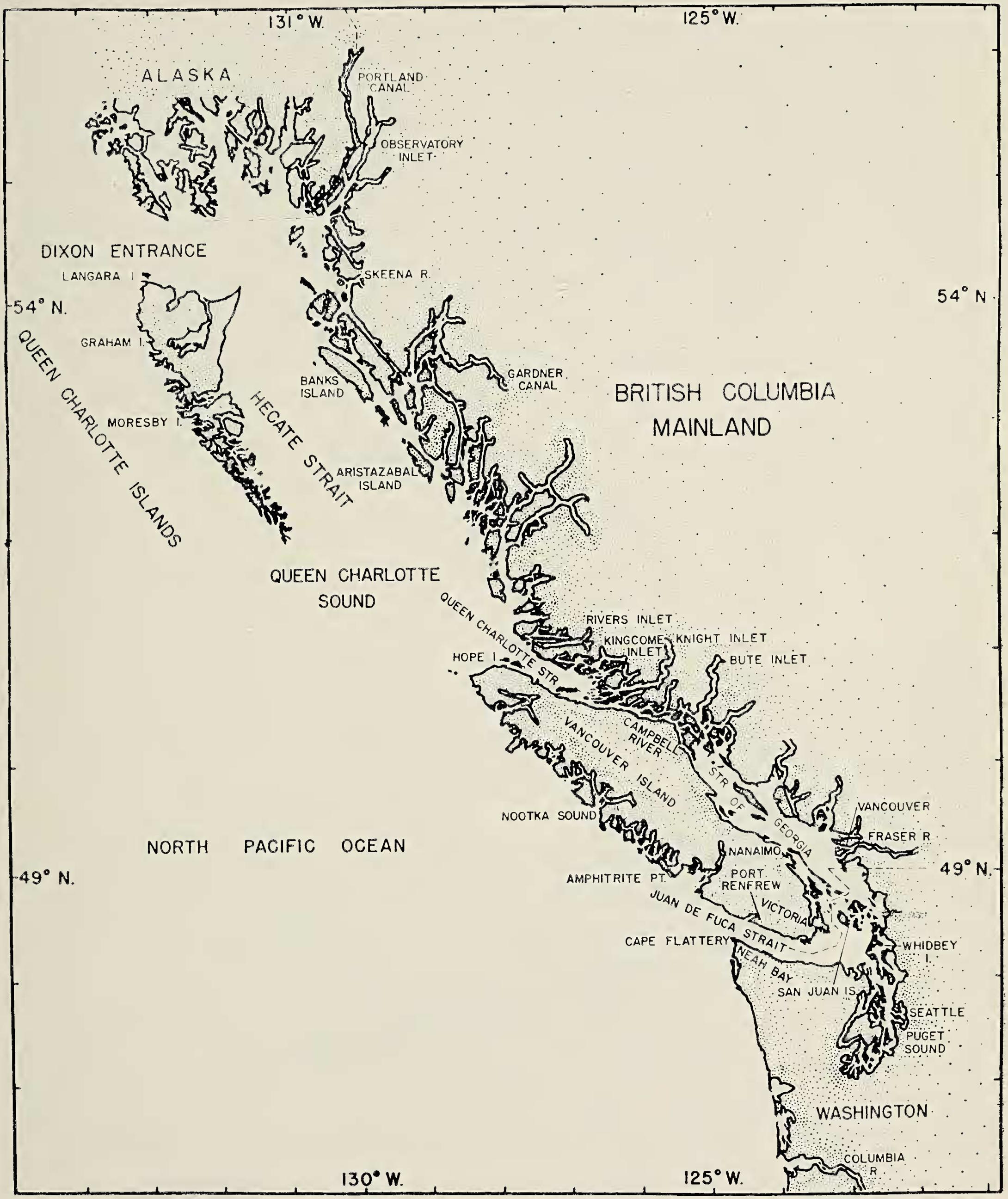


FIG. 1. Map of geographical features of the coast of British Columbia.

(1950) and his students in New Zealand. Some attempts have also been made to describe universal features of intertidal zonation throughout the world (Stephenson and Stephenson, 1949). At the same time there has been a tendency to place greater emphasis on the interrelationships between the various organisms.

Many of these intertidal studies have been of great value as an initial descriptive stage of investigation, and there is a need for further descriptive studies of this type in new and undescribed regions. However, the variety of systems of nomenclature and terms that have been proposed by marine ecologists to describe zonation, associations, and other ecological concepts has frequently only complicated the descriptive study rather than succeeded in explaining the observed phenomena. This has led to some confusion in terminology. It is a debatable point whether there can be such a thing as a universal system of classification beyond a generalized scheme, such as that proposed by Ekman (1935), and it is questionable whether some of the systems proposed can contribute further to progress in marine algal ecology even in regional studies without simplification or clarification. There have been a number of recent comprehensive papers dealing with various aspects of marine ecology which make it unnecessary to dwell at length on a review of the trends that have been followed more recently in marine algal ecology and the results that have been attained (Gislén, 1929, 1930; Feldmann, 1937, 1951; Fischer-Piette, 1940; Chapman, 1946, 1957; Doty, 1957; Hartog, 1959).

Although the shift in emphasis to the interrelationship of organisms was an important one, in some instances this approach has been responsible for excluding adequate concurrent studies of the physical and chemical aspects of the environment. It is for this reason that a case may be made for reassessing the status of marine algal ecology, and a critical evaluation of the steps to be taken to further its progress is timely. Perhaps what may be called a three-dimensional or an oceanographic approach can be used to analyze more precisely various factors in the marine environment and the relationship of these factors to the benthonic algae. Steps in this direction have been made more recently

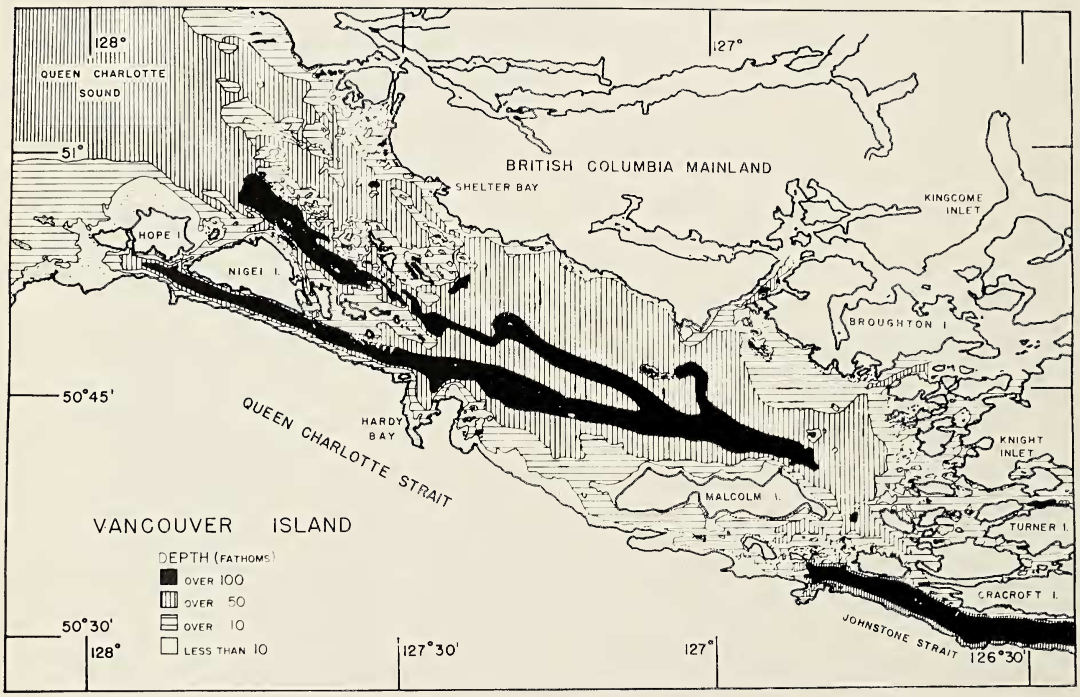


FIG. 2. Map of Queen Charlotte Strait showing depth contours.

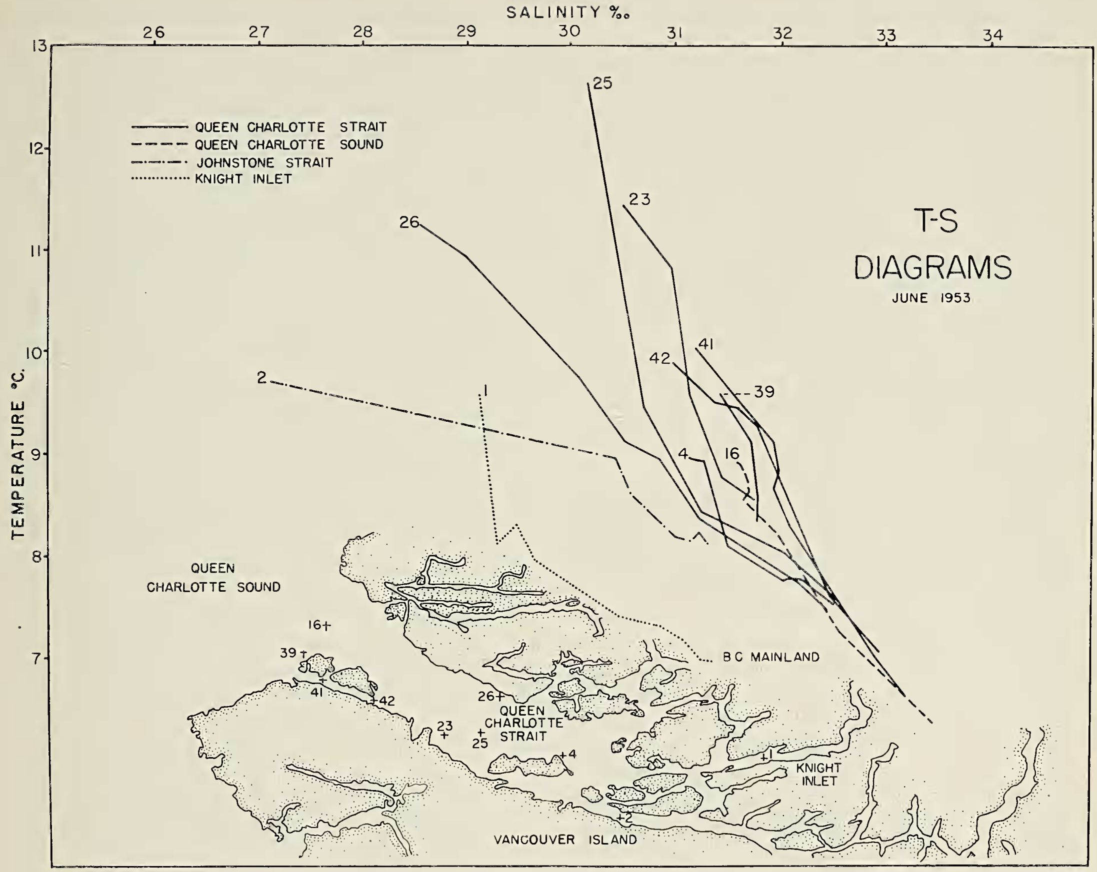


FIG. 3. T–S diagrams for stations in Queen Charlotte Strait and adjacent areas in June, 1953.

with some measure of success by Dawson (1945, 1951) in Baja California, Doty (1946) in Oregon, and Womersley (1956) in Australia.

The physical environment of the sea imposes problems of considerable magnitude which, in contrast to many land environments, presents formidable obstacles such as complex tidal and circulation patterns. In an effort to manipulate or simulate some aspects of this environment, both in the field as well as in the laboratory, the more generally available resources are soon taxed. Thus the methods that have been used in marine algal ecology have, in many instances of necessity, been crudely quantitative, less than ideal experimentally, frequently encumbered by terminology as a result of limited concurrent physical and chemical data, and sometimes they have failed to establish clearly the objectives being sought. As a result most of the efforts in marine algal ecology have been descriptive rather than functional in nature. As in most oceanographic work there is value in an approach from the grosser aspects to the particular. To the oceanographer the most complicated physical or chemical situation to explain may be the smallest unit of the environment with which he is faced. This is partly a problem of instrumentation. However, it is usually much easier to recognize significant discontinuities in properties, such as temperature, salinity, and even plankton distributions, over extensive areas of the ocean than in restricted or local regions. It is also easier to use such information in describing dynamic processes. Hence, it is suggested that more attention should be given to studies of the general distribution of various physical and chemical properties in the marine environment in an attempt to set up some workable hypotheses to account for observed distributions of marine algae. In this way we may hope to explain and account for biological phenomena rather than be satisfied by a description of the phenomena or by devising terms to describe them which do nothing more than give names to dynamic aspects of marine ecology much in need of logical explanation. With the recent increased activity in oceanography in the Pacific we may now hope for more abundant and usable data on some of the more general oceanographic properties of the North Pacific. In specific cases, particularly in more restricted areas, the ecologist will be forced to turn more attention to obtaining *in situ* physical and chemical data before further progress can be made.

One can arbitrarily start by summarizing all the factors in the marine environment as geological, physical, chemical, and biological. The way in which these are considered may be somewhat a matter of interpretation. Salinity, for example, may be considered directly, from a chemical standpoint, or indirectly as a physical factor responsible for changes in density and thus contributing to the pattern of circulation. Likewise, the nature of the substratum may be considered indirectly as a geological factor or directly as a physical or mechanical factor restricting or permitting establishment of benthonic organisms because of particle size. There has been much written on some of these aspects of ecological study in special cases, but it is suggested that, in a general over-all reassessment of the environment, an attempt be made to proceed from this more general position to the particular. This approach may initially lead only to the erection of further hypotheses, since the indirect or direct nature of the action of

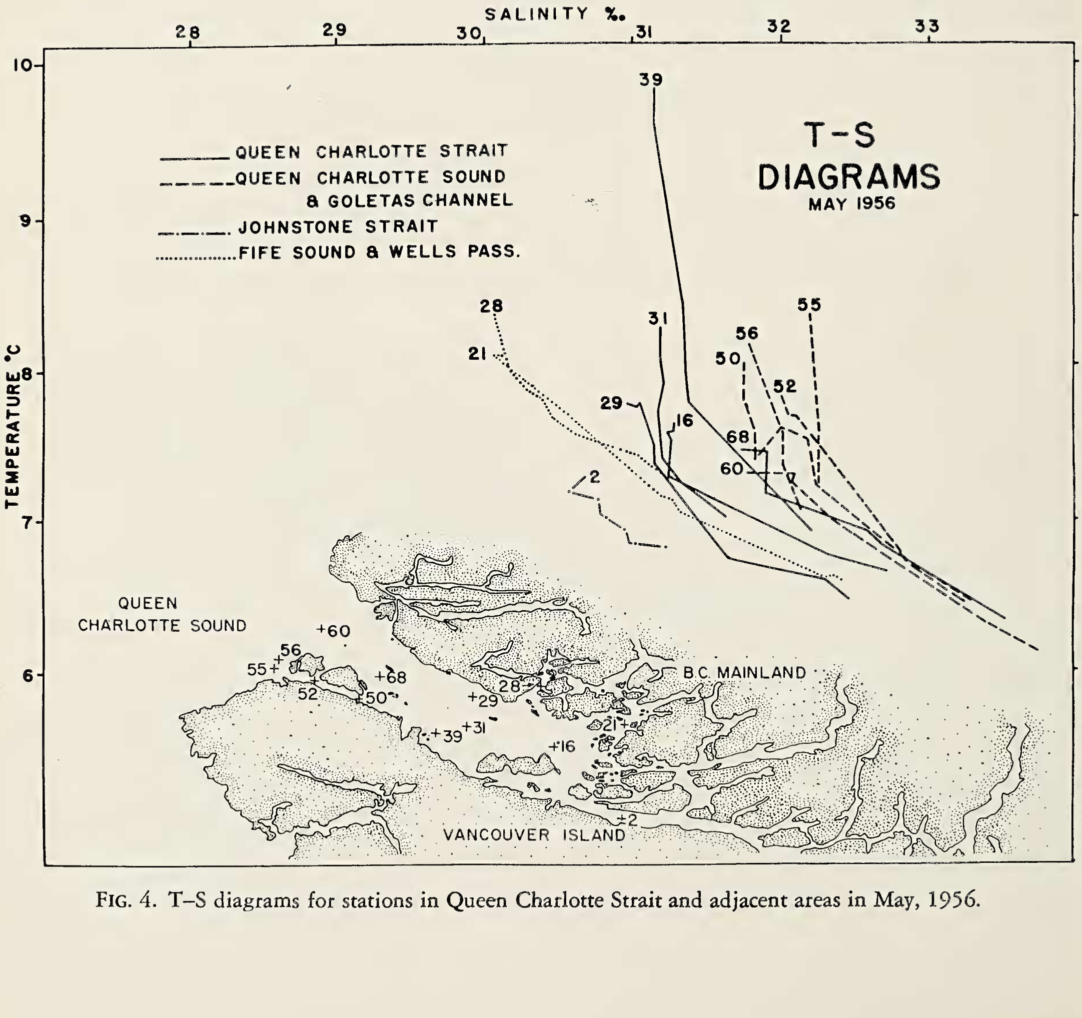


FIG. 4. T–S diagrams for stations in Queen Charlotte Strait and adjacent areas in May, 1956.

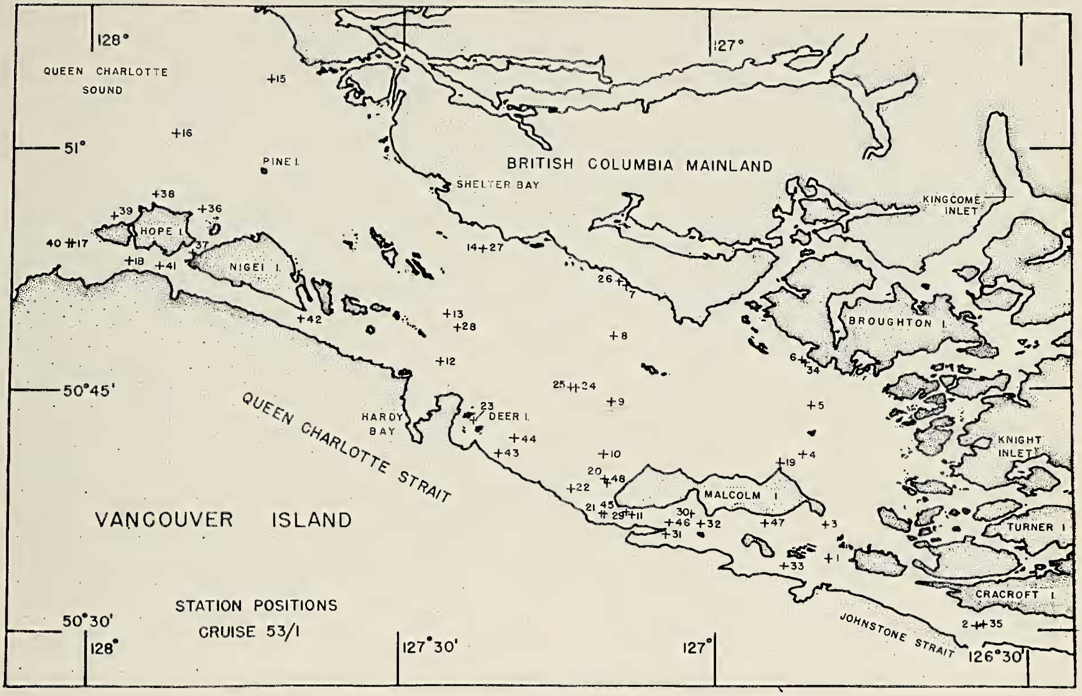


FIG. 5. Map of station positions in Queen Charlotte Strait in June, 1953.

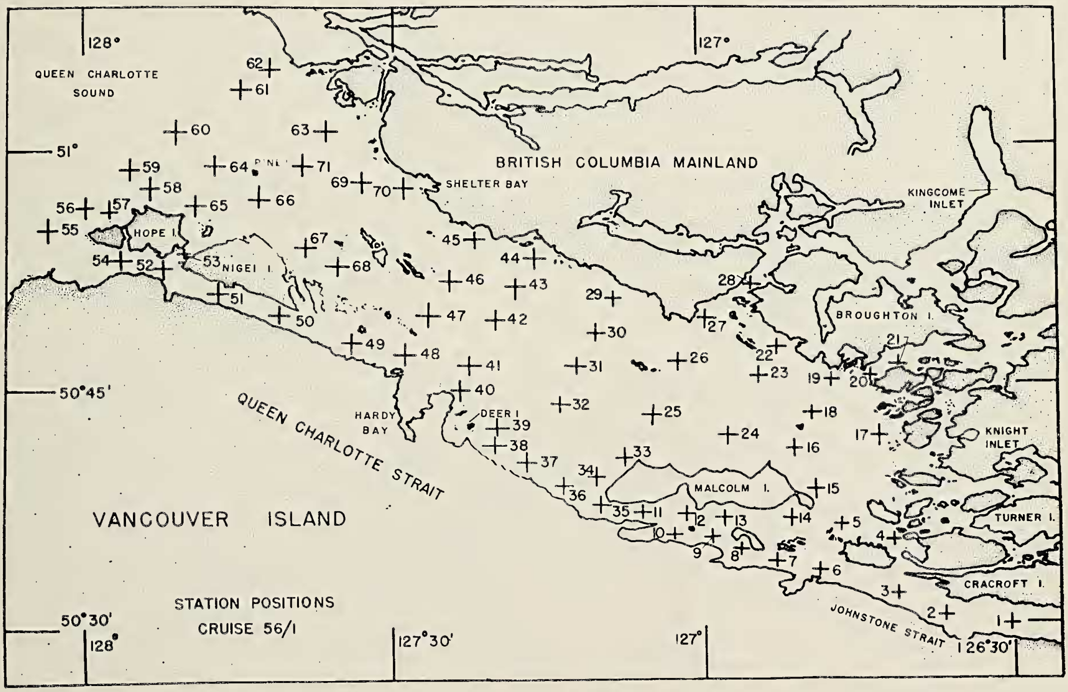


FIG. 6. Map of station positions in Queen Charlotte Strait in May, 1956.

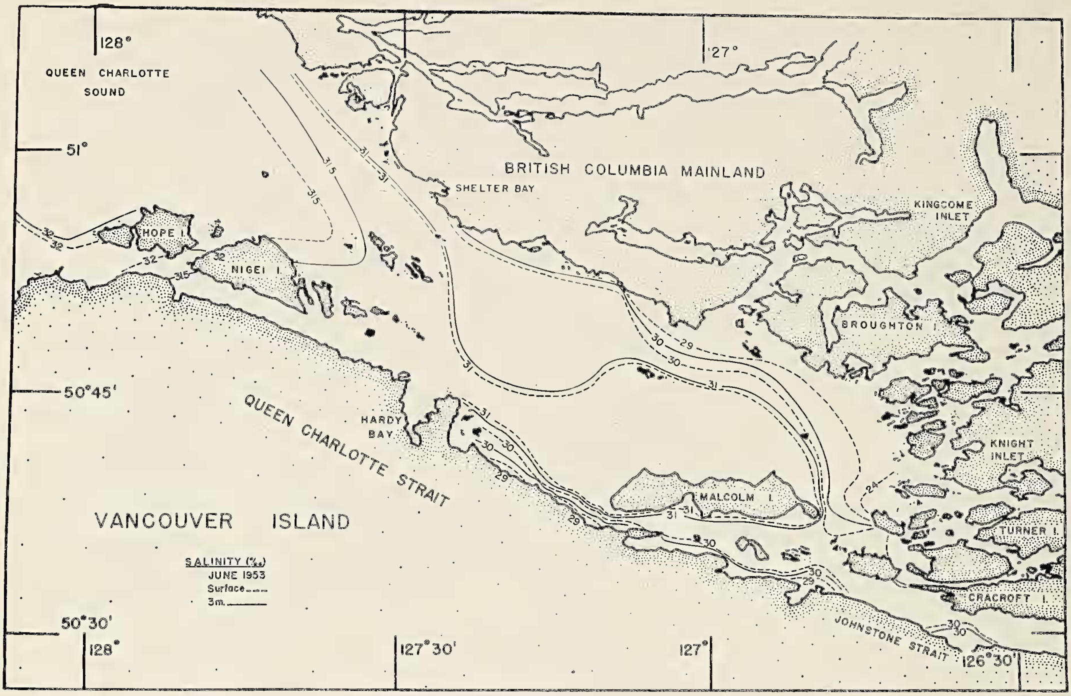


FIG. 7. Salinity distribution in Queen Charlotte Strait in June, 1953, at the surface and at a depth of 3 m.

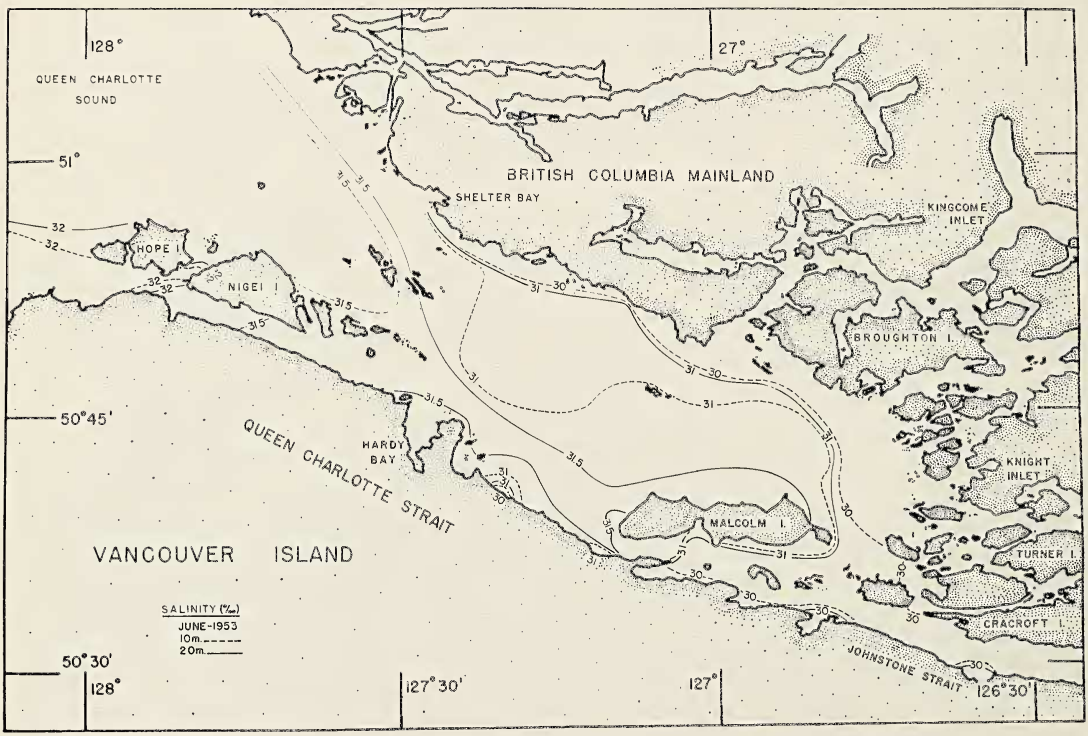


FIG. 8. Salinity distribution in Queen Charlotte Strait in June, 1953, at depths of 10 and 20 m.

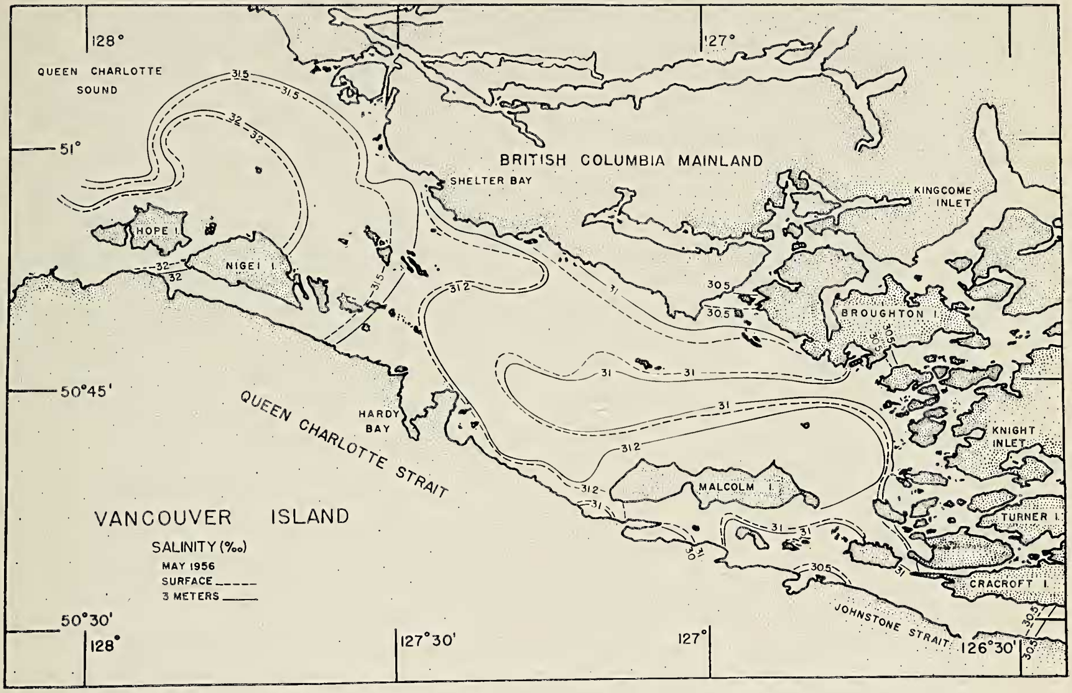


FIG. 9. Salinity distribution in Queen Charlotte Strait in May, 1956, at the surface and at a depth of 3 m.

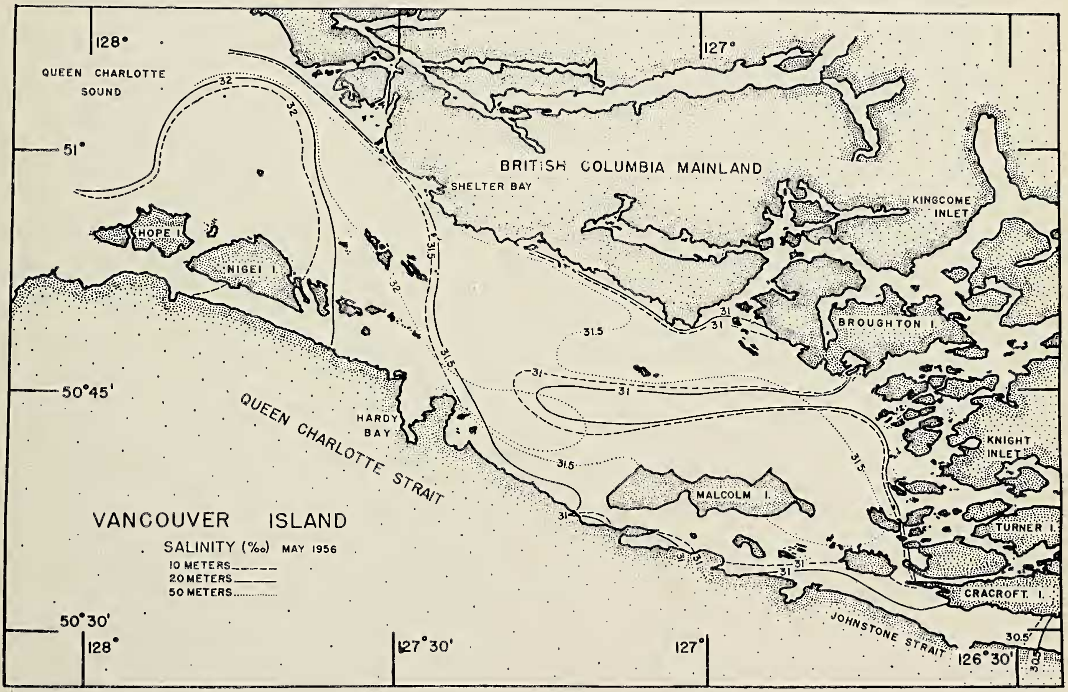


FIG. 10. Salinity distribution in Queen Charlotte Strait in May, 1956, at depths of 10, 20, and 50 m.

any particular factor in the environment may ultimately be established only by experimental work either in the field or in the laboratory. In some regions where the algal flora is well known taxonomically the descriptive aspect can and has been undertaken and the time has come when further progress in such an area can only be expected by undertaking experimental field and laboratory studies. In some regions, even where the flora may be well known, inadequate physical and chemical data militate against further progress and even the advancement of tenable hypotheses. Only when such hypotheses are put forward, based on a correlation of the observational data, can one anticipate and justify embarking on an experimental field and laboratory approach in an attempt to solve problems relative to the distribution of marine algae.

This is the approach that is outlined here in studies on marine organisms and, particularly on the marine algae, being carried out on the coast of British Columbia, some aspects of which will be considered here in detail. As a step in the direction of increasing our knowledge of the entities which comprise the tools of the algal ecologist and of completing this descriptive phase of the study of the marine benthonic algae, an annotated check list has been completed for the coast of British Columbia and northern Washington (Scagel, 1957). Based on this list, further studies are now in progress to augment the existing data on the marine flora of British Columbia, not only on distributions but also on life histories, growth, reproduction, and seasonal aspects. These fundamental studies are basic to all other aspects of ecological research, especially when an attempt is made to use specific organisms as indicators of oceanographic conditions.

Not only does this descriptive phase require an adequate consideration of the taxonomic aspects, but also a complete description of the other factors in the environment is needed. With increased activity recently and currently in general oceanographic studies of the North Pacific by a number of organizations on the Pacific

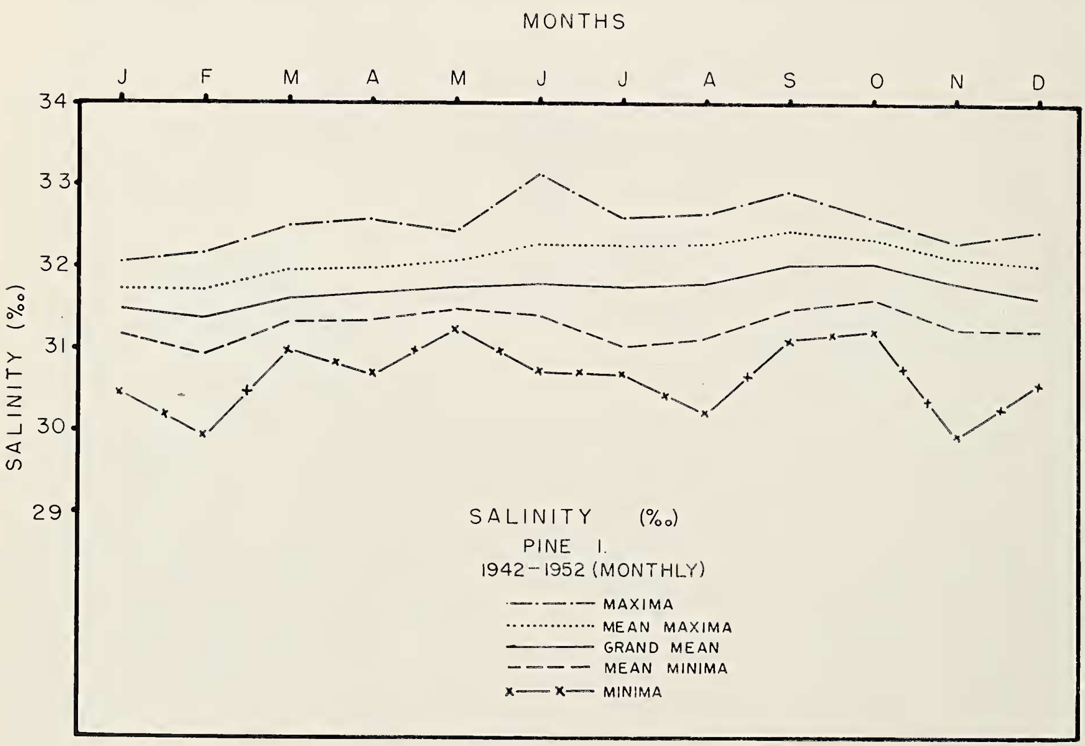


FIG. 11. Monthly salinities at Pine Island for the period 1942–52.

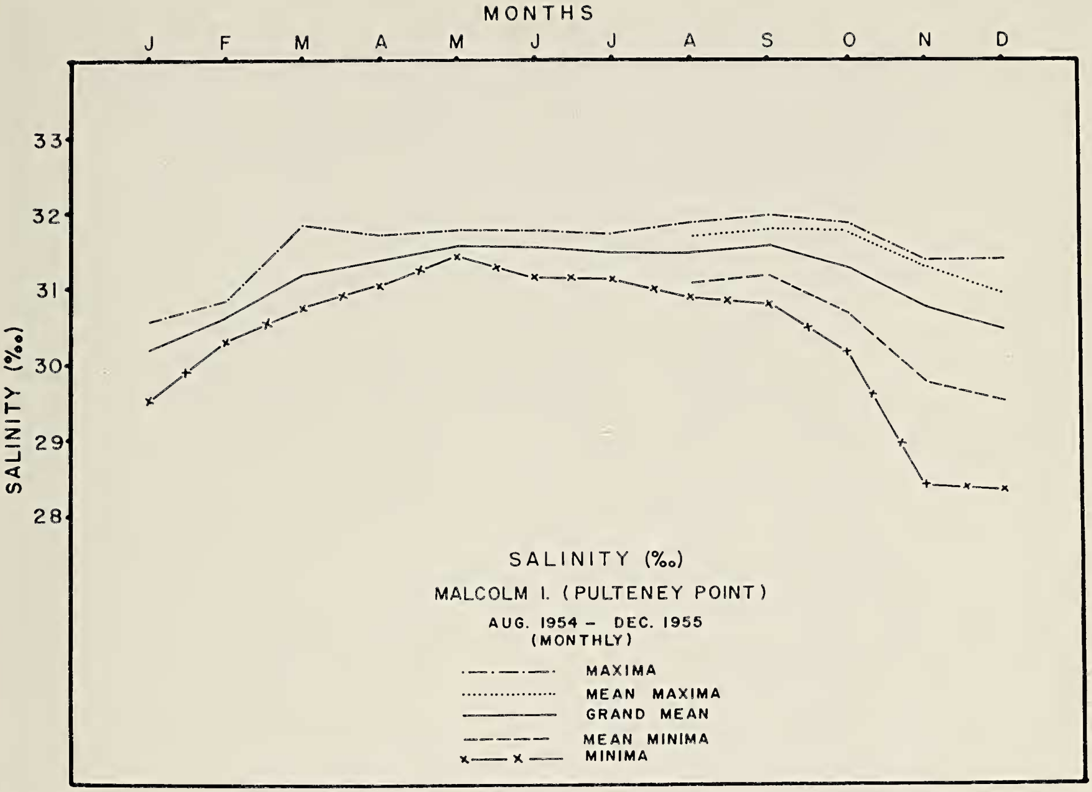


FIG. 12. Monthly salinities at Pulteney Point, Malcolm Island, for the period 1954–55.

Coast of Canada, in Japan, and in the United States, there has resulted a considerable body of scientific knowledge but it is still far from adequate for the ecologist, particularly for one interested in coastal dynamics. Circulation patterns, temperature, salinity, oxygen, and in some areas phosphate, silicate, and nitrate distributions are fairly well known in a broad and general sense, but at the present time these oceanographic data are known in sufficient detail for few restricted areas. Knowledge of the distribution of other chemical constituents and to a large extent even of the plankton composition, distribution, and activity is almost completely lacking. Much more information is needed in order to tackle many problems relating to specific distributions and to set up field and laboratory studies to test hypotheses.

It is already apparent that much can be done experimentally both in the field and in the laboratory with the benthonic algae. Many of the problems encountered by the ecologist dealing with large marine algae present unique culture problems both in the field as well as in the laboratory. Some studies of growth and reproduction, particularly of some of the larger Laminariales, have been done in this region both in the field (Scagel, 1948) as well as in the laboratory. Although the size of many of the cold-water marine algae adds special problems, at least some of the stages can be carried out to the point where transplant experiments can be made from the laboratory into the sea for further study. Transplant experiments of natural populations of juvenile stages, at least of these larger marine algae, even in the case of *Macrocystis*, are quite feasible.

The successful use of the experimental approach in the laboratory is primarily dependent on having facilities for maintaining temperature and light control, although the size of plants may again present certain special problems. Cultures of Laminariales have been maintained in controlled-environment tanks at the

University of British Columbia for as long as a year, during which the complete sexual generations were grown and the young sporophytes reached a length of 14 in., well past the stage where secondary morphological characteristics had developed to a point permitting positive identification. These studies have permitted indisputable identification of the sporophytes to genus, and in some cases to species. The study of cultures in this group suggests that much of the early work on gametophytes in the Laminariales and in fact even on the early sporophytes may be in some question. In most of the early studies reported in the literature, plants were not grown long enough to establish beyond doubt the characteristic secondary morphological features of the sporophytes of the genera from which zoospores were intially obtained. In the presence of contaminating zoospores of other species which can soon supplant the original species under study, there is no other way of establishing that the same species or even the same genus in the Laminariales was obtained in the sporophyte generation succeeding the gametophyte generations in culture.

It would be remiss not to mention much of the worthwhile physiological work that has been done on marine algae and other organisms. However, there is a need for a great deal more physiological work, particularly of the type done by Gail (1918, 1919, 1922) in an attempt to relate physiological processes more specifically and directly to the environment and ecological problems encountered in the field. In physiological studies there is frequently a tendency to proceed more and more deeply into special aspects of the physiological behaviour or the biochemistry of an organism under artificial conditions. Although this information is very often of great value there is a very real need to project back to the field and attempt to explain behaviour under the conditions existing in the natural environment. The statistical approach, as illustrated by Berquist's (1959) revealing study of *Hormosira*, has also been little used as yet.

Almost all of the quantitative aspects of the productivity of the benthonic algae in this area have related to species of economic interest (anon., 1947, 1948*a*; Scagel, 1948; Hutchinson, 1949). These studies have dealt largely with harvestable quantities and distributions, and have contributed little to an evaluation or an explanation, in terms of oceanographic factors, of the causes for this production.

Obviously the ideal of a functional interpretation in the ecology of marine benthonic algae is dependent on an adequate and balanced knowledge of all of the foregoing aspects—of the qualitative and quantitative features of both the organisms and the environment. Many, much needed data are still lacking. An attempt to follow this line of investigation has been pursued on the coast of British Columbia and in a somewhat more restricted area at the north end of Vancouver I. in Queen Charlotte Strait. Further detailed work is in progress in the Strait of Juan de Fuca at the south end of Vancouver I. between Vancouver I. and northern Washington. The study in Queen Charlotte Strait forms the major part of this paper.

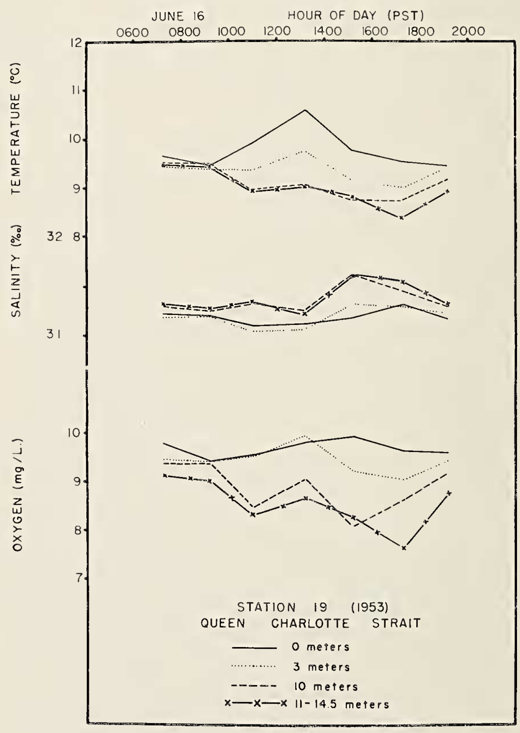


FIG. 13. Fluctuations in temperature, salinity, and oxygen at various depths near Malcolm Island at station 19 (1953).

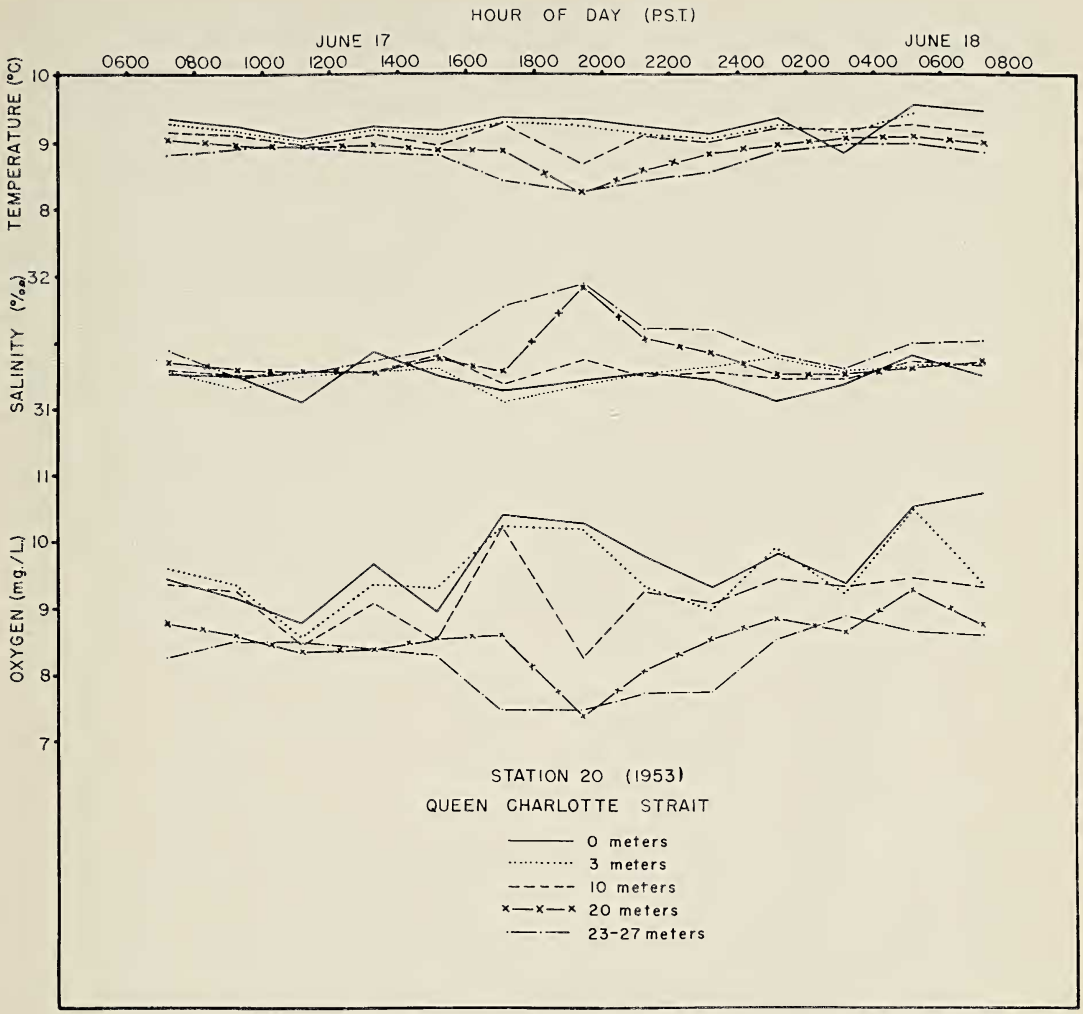


FIG. 14. Fluctuations in temperature, salinity, and oxygen at various depths near Malcolm Island at station 20 (1953).

The more detailed physical and chemical data presented in this paper for the Queen Charlotte Strait area were obtained during two cruises, one (53/1) on the C.G.M.V. "Cancolim II" in 1953 (anon., 1955*a*) and the other (56/1) on the C.N.A.V. "Ehkoli" in 1956 (anon., 1956*a*). The stations occupied during these two cruises are indicated in Figures 5 and 6, respectively. Further less detailed observations were made on a cruise (57/6) in May, 1957, on the C.N.A.V. "Clifton" (anon., 1958). In analyzing the seasonal characteristics and annual fluctuations of temperature and salinity that occur, reference has been made to the data obtained in the area from the daily records (anon., 1944, 1946, 1948*b*, 1949, 1950, 1951, 1952*b*, 1953*a*, 1955*c*, 1956*c*) and data reports of the Hecate Strait Project (anon., 1955*b*, 1955*d*, 1955*e*, 1956*b*) of the Pacific Oceanographic Group. Meteorological data have been obtained from the Meteorological Observations in Canada (anon., 1953*b*), and tidal data were taken from the Pacific Coast Tide Tables (anon., 1952*a*). Chart data have been taken from charts of the Canadian Hydrographic Office and the British Admiralty. Some additional physical and chemical (anon., 1954; Pickard and McLeod, 1953) and geological data (Dawson, 1880, 1881*a*, 1881*b*, 1888, 1897; Bostock, 1948) have been referred to in the literature. Earlier biological observations and collections, which form part of the background for this paper, were made in the area in 1946 (anon., 1947, 1948*a*) and 1947 (Scagel, 1948). The results of a study of the phytoplankton and zooplankton collections which were also made during the same cruises will be presented in a subsequent paper.

## GENERAL ECOLOGICAL CHARACTERISTICS OF COASTAL REGION

The Pacific Coast of Canada is ideally suited to a study of benthonic organisms and the effect of oceanographic factors on their distribution both in the intertidal and the subtidal zones. Although the coast of British Columbia (Fig. 1) is only about 600 mi. long, proceeding directly from the Strait of Juan de Fuca to Dixon Entrance, if all its various ramifications are included there is a coastline estimated at about 16,900 mi. in length. The tidal amplitude in this region is great, ranging from about 11 ft. at the southern boundary to nearly 26 ft. at the northern boundary. As a result of thorough mixing in the coastal region the upper zone in this area, except for a few local anomalies, is characteristically rather uniform in temperature at any one period and fluctuations occur within narrow limits. The annual range in temperature of the seawater near the surface is from about 6° to 18°C. On the other hand, because of the runoff from large rivers, especially through the long mainland inlets, there are conditions ranging from practically fresh water at one extreme to full ocean salinity of about 34 ‰ at the other.

Throughout the coast the physical nature of the substratum, ranging from mud and sand at one extreme to solid rock at the other, determines to a large extent the organisms which are found in a specific area. However, a comparison of the flora and fauna on various types of bottom is possible in a number of regions which are otherwise oceanographically rather similar. This permits a correlation of the distribution of a wide variety of plants and animals with other physical and chemical factors of the environment. The oceanographic conditions characteristic of the coast provide an ideal area in which to study the distribution of marine benthonic organisms particularly in relation to salinity over a rather extensive geographic area.

## GEOLOGICAL CHARACTERISTICS

### *General Coast Features*

The Coast Mountains of British Columbia, which run along the whole length of the prov-

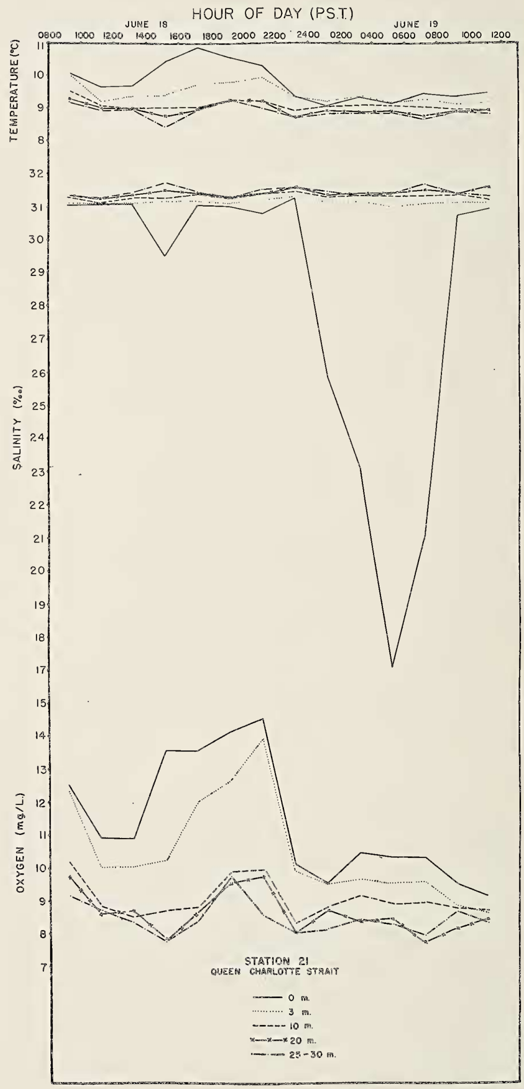


FIG. 15. Fluctuations in temperature, salinity, and oxygen at various depths near the Klucksiwi River at station 21 (1953).

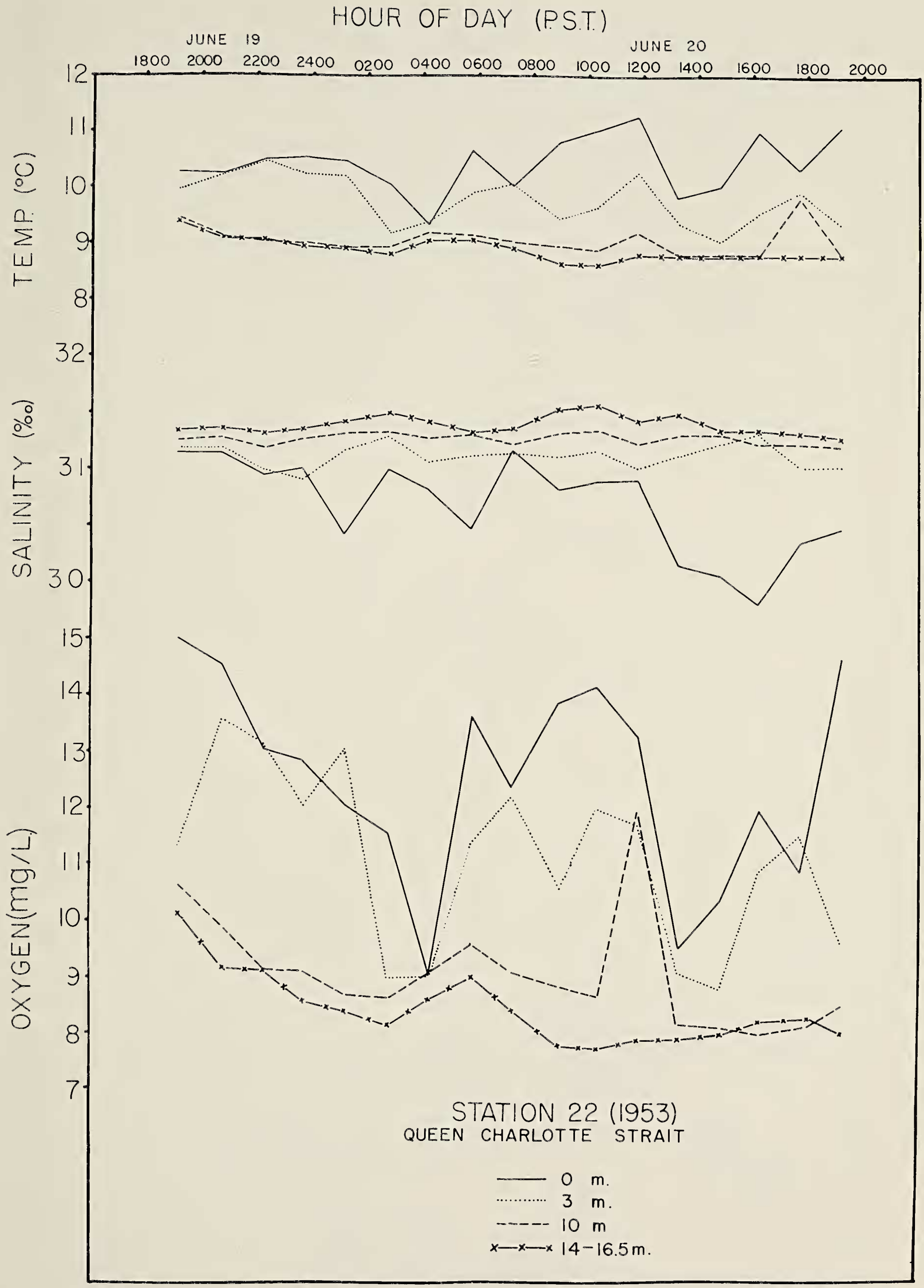


FIG. 16. Fluctuations in temperature, salinity, and oxygen at various depths near the Klucksiwi River at station 22 (1953).

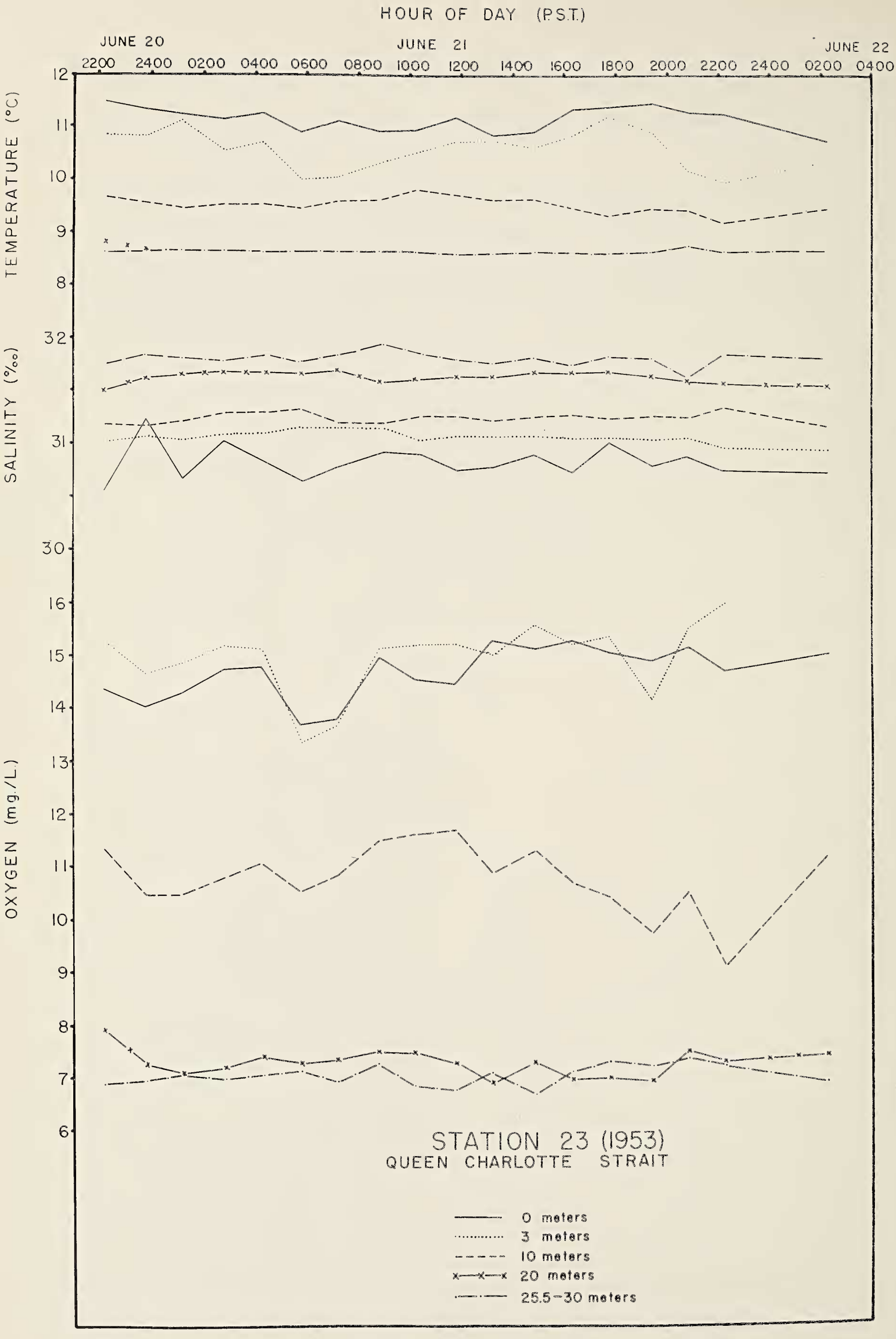


FIG. 17. Fluctuations in temperature, salinity, and oxygen at various depths near Deer Island at station 23 (1953).

ince with an average width of about 100 mi., constitute the mainland coast. Although not as rugged as elsewhere in the Cordillera, the western side of the Coast Mts. rises from the sea precipitously to summits in places exceeding 8,000 or 9,000 ft. Several rivers, which rise in the plateau country to the eastward, flow completely across this range to the Pacific, where the lower parts of their valleys, as well as those of many streams originating in the mountains themselves, continue in the extensive system of fjords along the mainland of British Columbia (Fig. 1). These sediment-filled systems of valleys with steep slopes and numerous deltas can be traced in some places even through the coastal archipelago, which represents a partly submerged margin of the Coast Mountains. West of the Coast Mountains, and in a partly submerged condition, lies another chain, the Insular Mountains, of which Vancouver I. and the Queen Charlotte Islands are projecting ranges. This outer chain stands on the edge of the continental platform with the great depths of the Pacific seaward from it. Between these

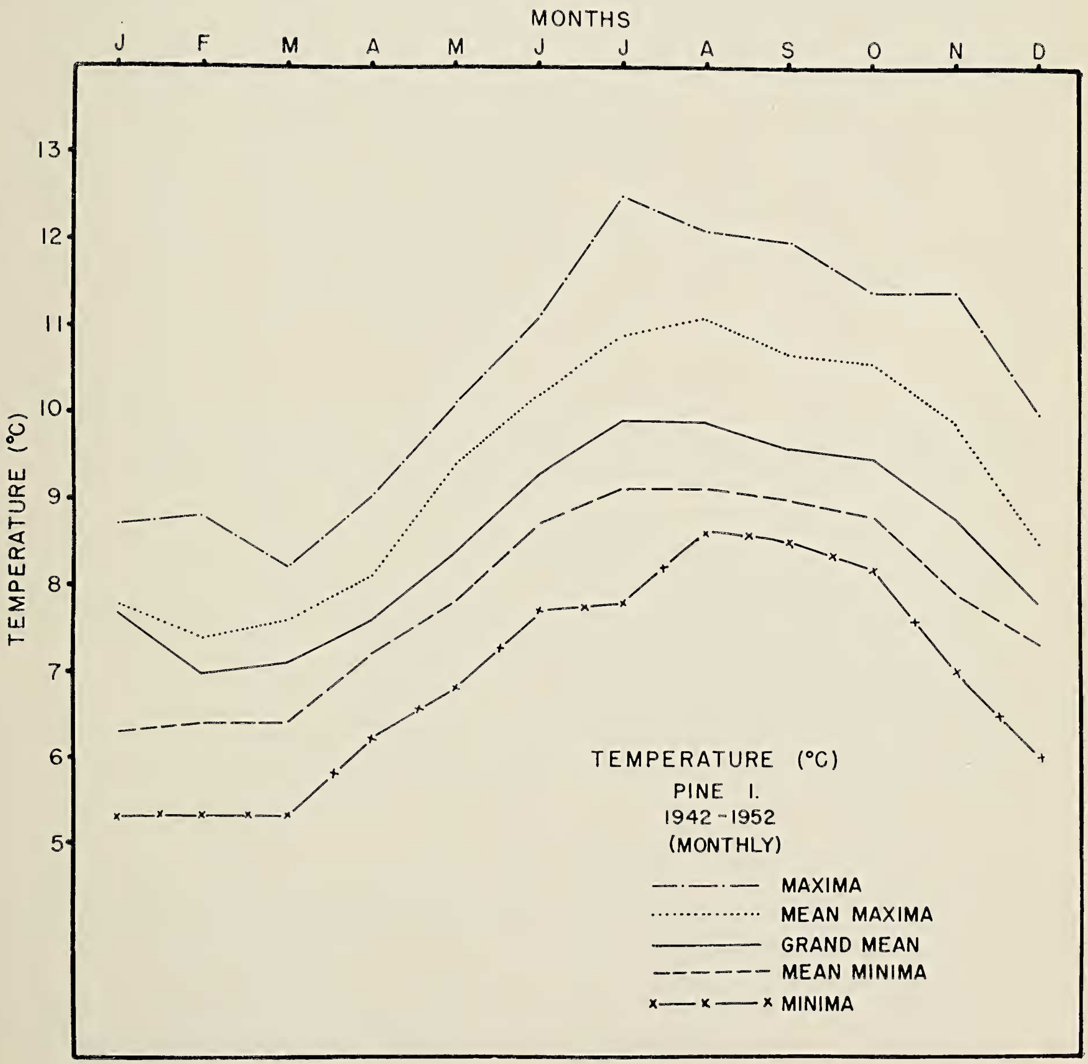


FIG. 18. Monthly temperatures of seawater at Pine Island for the period 1942–52.

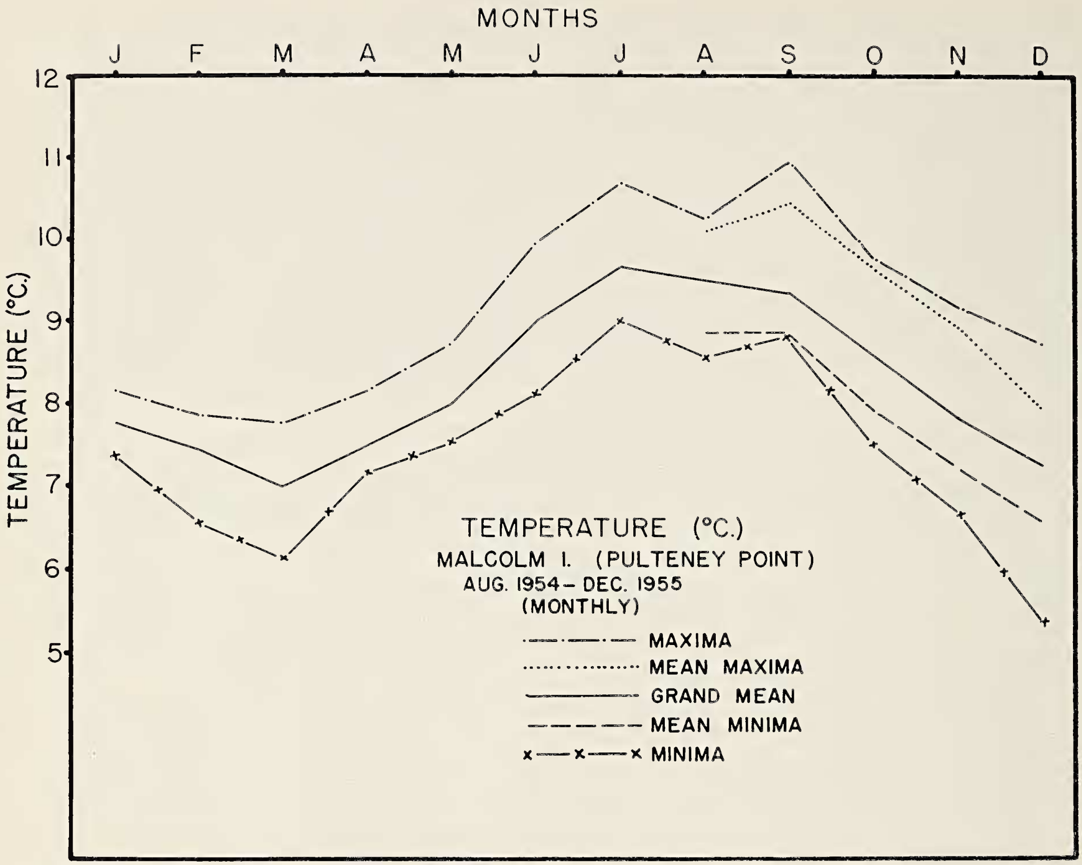


FIG. 19. Monthly temperatures of seawater at Pulteney Point, Malcolm Island, for the period 1954–55.

two ranges lies the Coastal Trough, part of a great depression extending intermittently northwestward from the Gulf of California through the Puget Sound–Williamette lowland and on into Alaska. In British Columbia this great valley is largely submerged and comprises the extensive areas of the Strait of Georgia, Queen Charlotte Strait, Queen Charlotte Sound, and Hecate Strait (Fig. 1).

The Coast Mountains consist largely of Mesozoic rocks ranging from Triassic to early Tertiary and are composed of principally granitic rocks with some included masses of Mesozoic and Palaeozoic strata. The rocks of the Vancouver I. Ranges are composed conspicuously of masses of Triassic and Jurassic lava and volcanic products, lesser contemporaneous sediments with subordinate amounts of later granitic rocks, and marine and continental Cretaceous

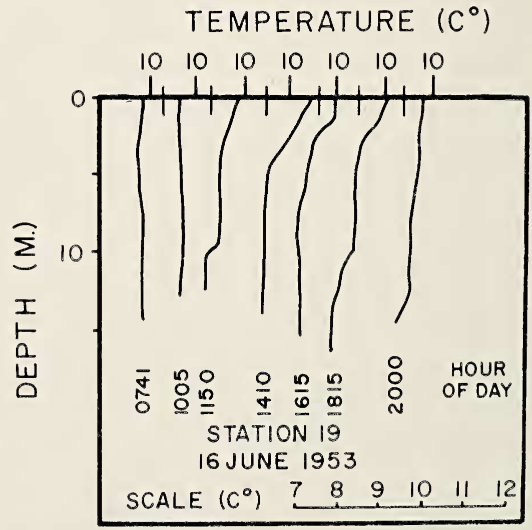


FIG. 20. Temperature profiles at station 19 (1953) near Malcolm Island from bathythermograph traces.

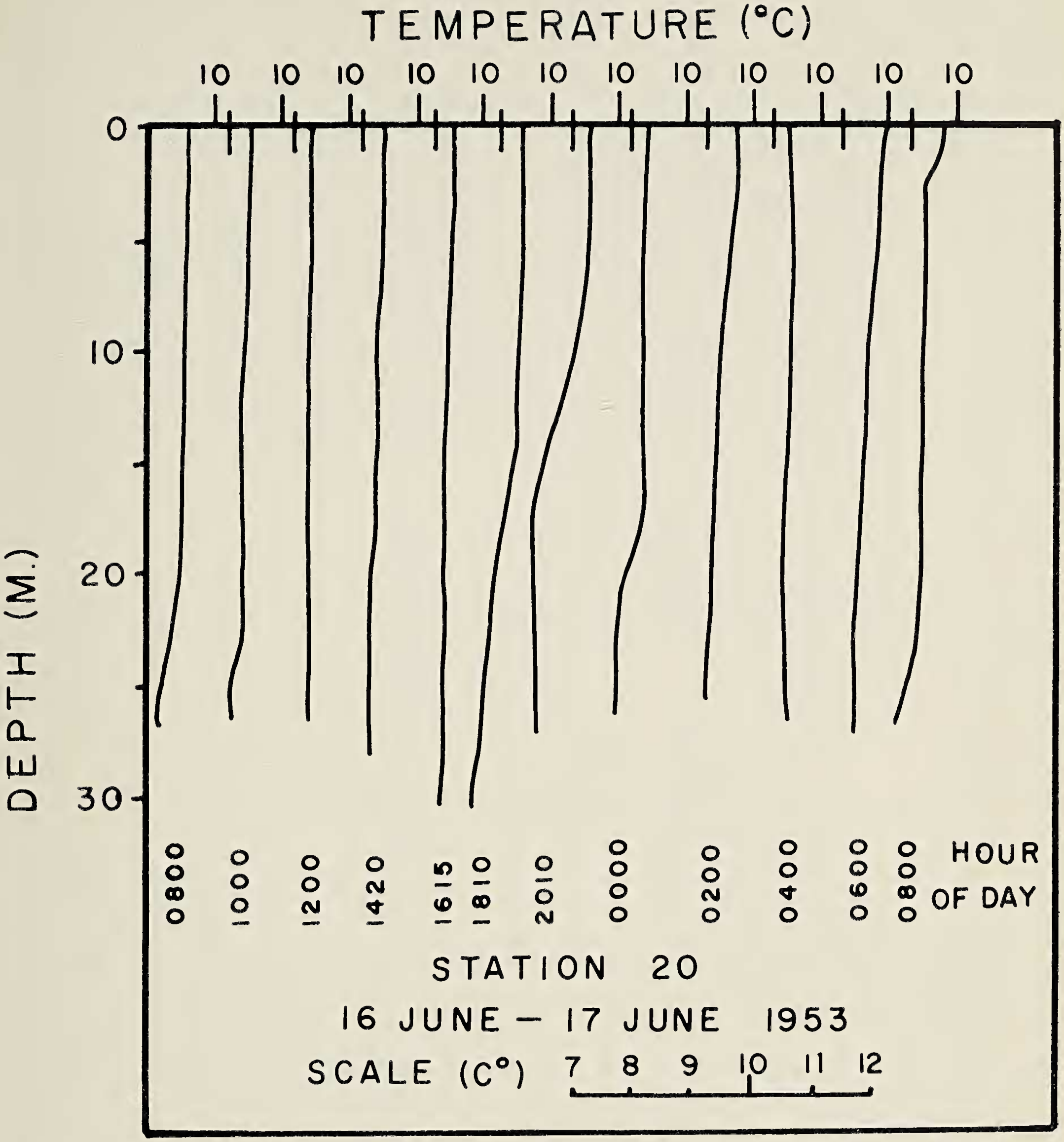


Fig. 21. Temperature profiles at station 20 (1953) near Malcolm Island from bathythermograph traces.

sediments which have participated in its folding. Horizontal Miocene beds occur along some parts of the shore.

*General Features of Queen Charlotte Strait*

Along the mainland portion of Queen Charlotte Strait (Figs. 1, 3) the rocks are chiefly Jurassic and intrusive, composed of granodiorite, chiefly quartz diorite. Parts of the island groups near the entrance to the Strait, including Hope I. and Nigei I., include some intrusive rocks similar to those on the mainland side, but the major part of the north end of Vancouver I. is composed of Triassic to Jurassic rocks. In this latter region argillites, lavas, tuffs, breccia, sandstones, and limy siltstones are common. A smaller portion of the east coast of Vancouver I. from Hardy Bay southward almost to Johnstone Strait is Cretaceous (chiefly Upper Cretaceous), with shales and sandstones.

The rocks are heavily glaciated throughout almost the whole coastal area. The Queen Charlotte Strait area was heavily glaciated during the Pleistocene, which fact is particularly evident in the vicinity of Deer I., where northwestern slopes are comparatively rough in contrast to the grooved and polished vertical or near vertical faces on southeastern parts. Well-stratified deposits of clays, silts, and sands occur, particularly toward the east end of the Strait and along the Vancouver I. side. Cormorant I., Harwood I., and Malcolm I. are also examples of these deposits. In some places cliffs of these deposits border the shoreline, with extensive accumulations of boulders at the base. In such regions the boulders, which occur in great abundance along the beaches, are probably erratics derived from morainic material.

Although the detailed geology of Queen Charlotte Strait region is not well known supratidally, it is even less well known subtidally. The general features described, however, indicate the wide variety of substrata available for the attachment of benthonic organisms, particularly in the intertidal and shallower subtidal zones. This variety in the physical nature of the sub-

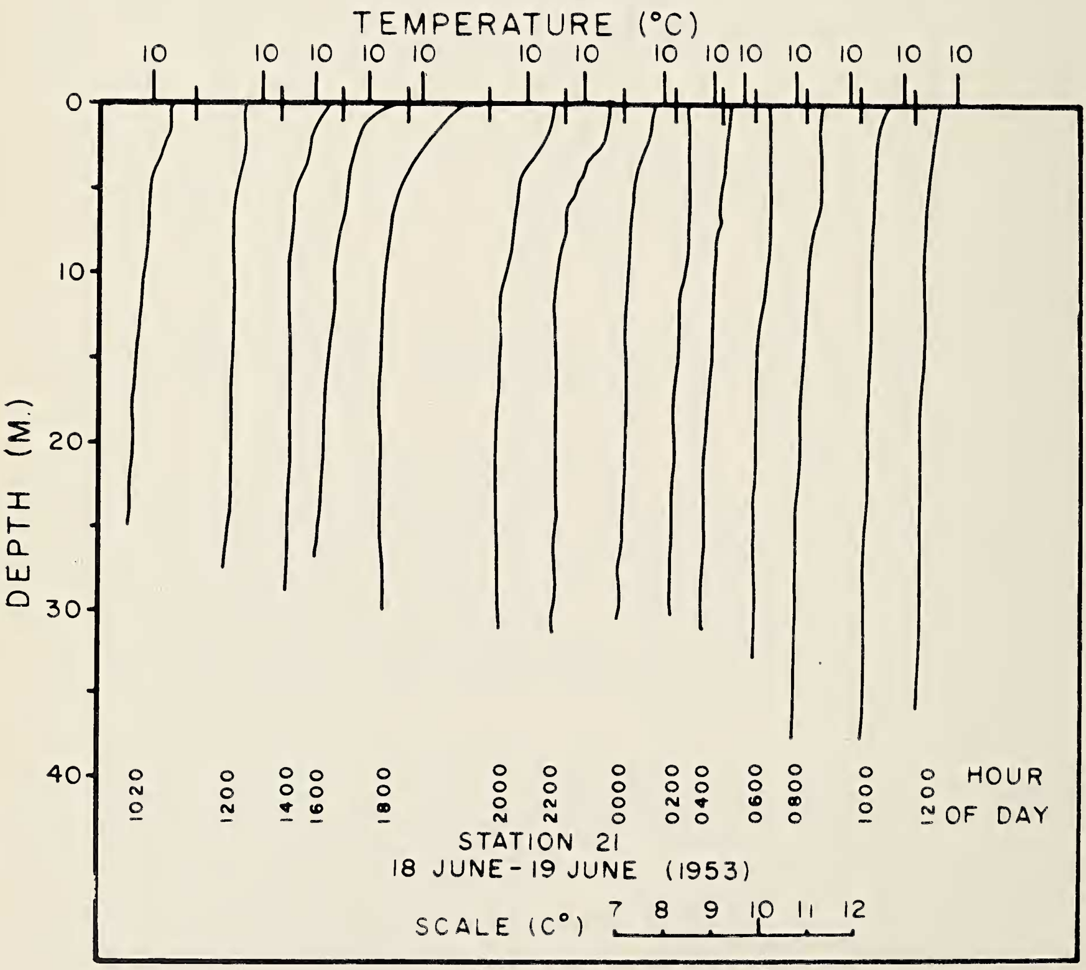


FIG. 22. Temperature profiles at station 21 (1953) near Malcolm Island from bathythermograph traces.

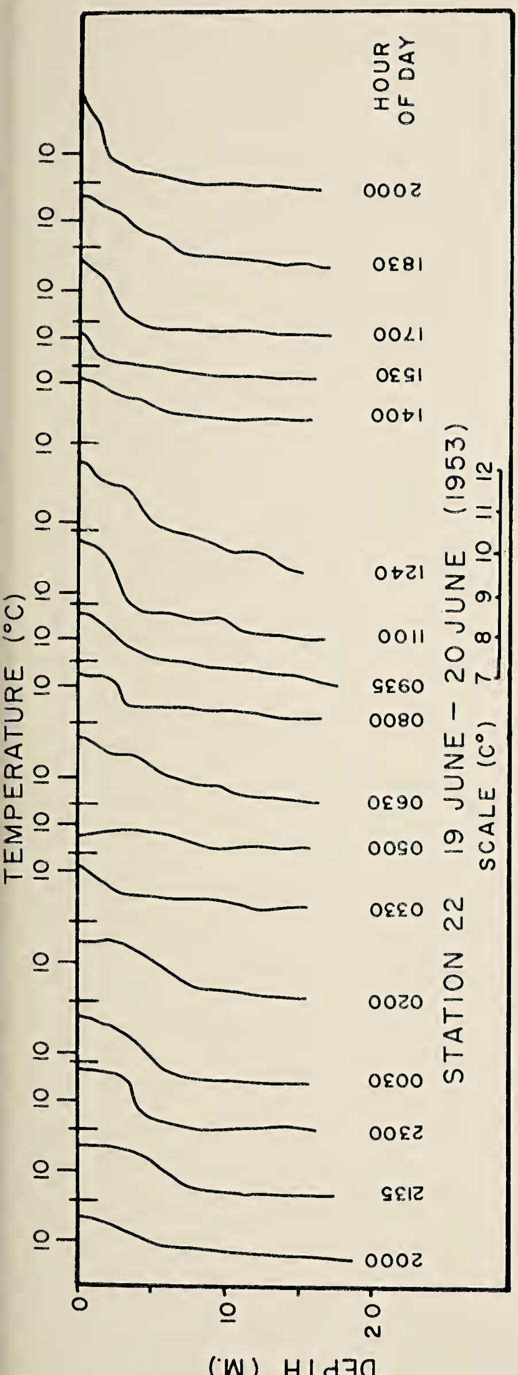


FIG. 23. Temperature profiles at station 22 (1953) near Malcolm Island from bathythermograph traces.

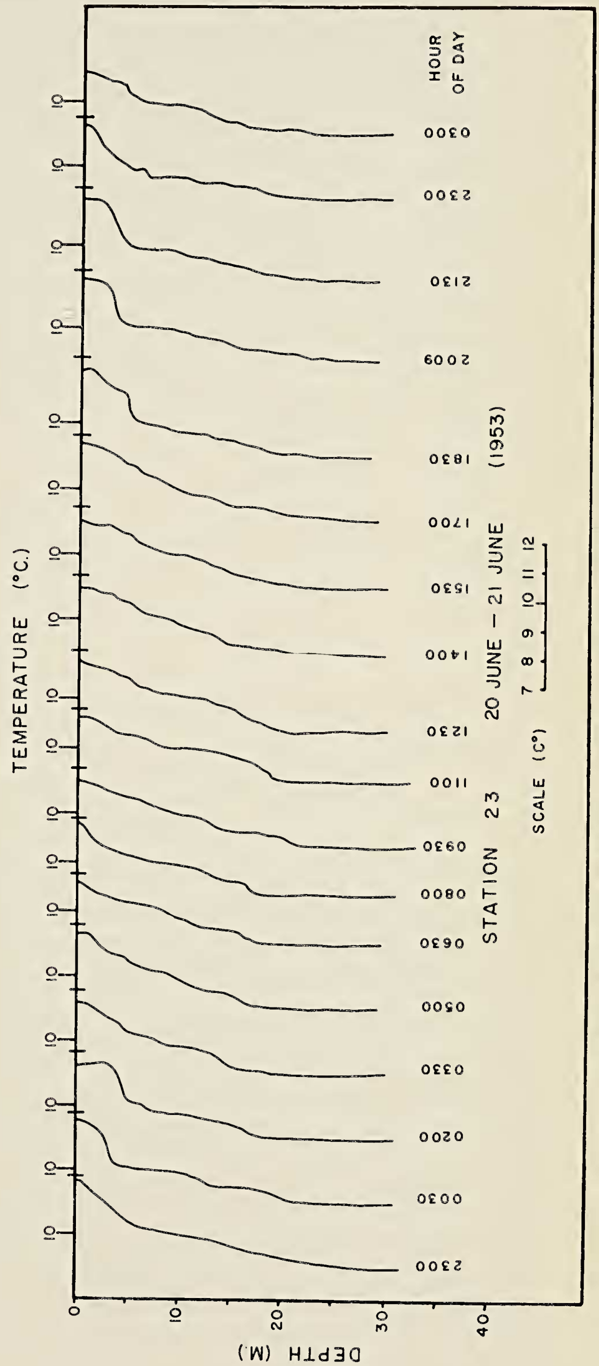


FIG. 24. Temperature profiles at station 23 (1953) near Deer Island from bathythermograph traces.

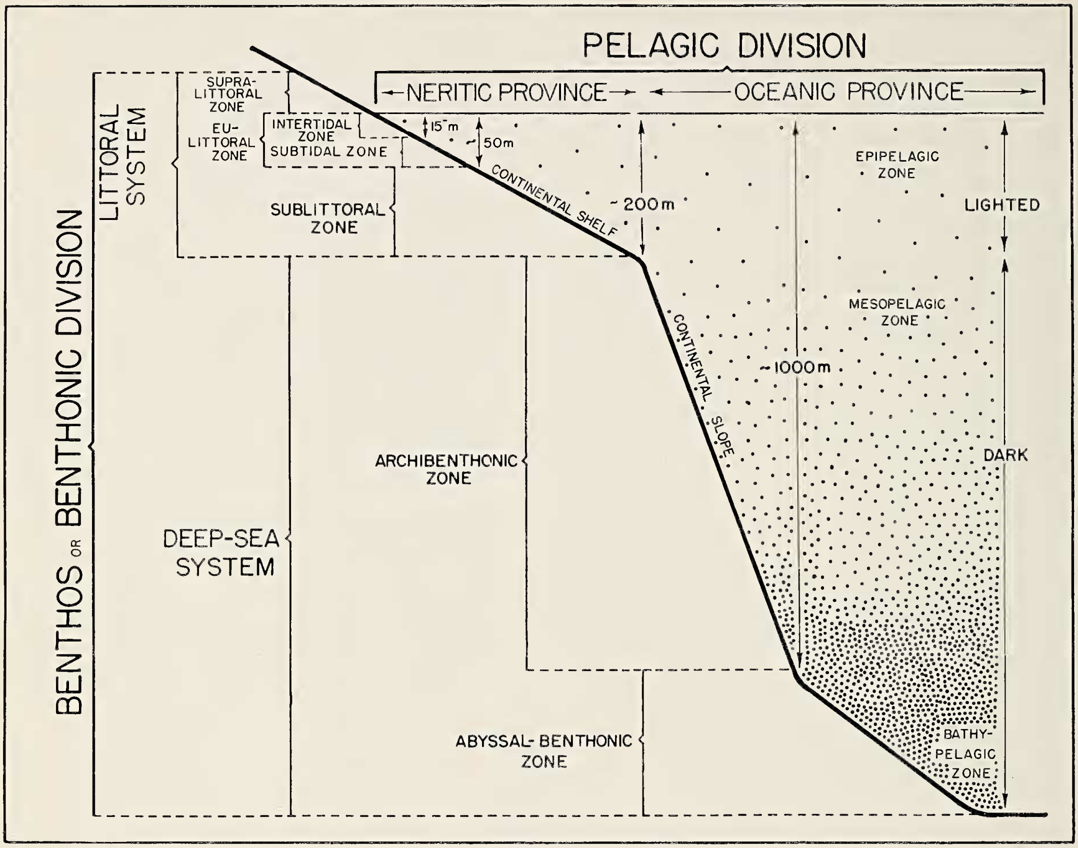


FIG. 25. Diagrammatic representation of regions of marine habitat (modified after Ekman, 1935).

stratum is apparent not only geographically in the area but also vertically. In the deeper water soft mud bottoms predominate but sand and gravel are also found, and in the shallower areas sand, mud, gravel, pebbles, boulders, and solid rock are all found to varying extent, particularly along the Vancouver I. side of the Strait. In the shallower regions, however, a solid rock or bouldery substratum predominates. The nature of this rocky substratum in Queen Charlotte Strait is equally varied. There are igneous as well as sedimentary and metamorphosed substrata. There are basalts, dolerites, trachytic rocks, hard sandstones or quartzites, shales, conglomerates, argillites, fine-grained to crystalline, commonly cherty limestones mixed with feldspathic rocks, and dioritic and granitic fragments are also common.

The preceding brief summary of the general geological features of the area indicates the present status of published knowledge (Bostock, 1948; Dawson, 1880, 1881*a*, 1881*b*, 1888, 1897) concerning the Queen Charlotte Strait region.

*Bottom Topography of Queen Charlotte Strait*

Although soundings are still incomplete for the area, a study of the bottom topography (Fig. 2) in Queen Charlotte Strait indicates extensive shallows, particularly along the Vancouver I. side of the Strait and around Malcolm I. In this region an abundant and varied intertidal and subtidal flora and fauna are supported. In the central part of the Strait and between Nigei and Vancouver islands (Fig. 2), there are deeper channels exceeding 100 fathoms. The water in these deeper channels is not continuous, however, with the deep waters of the mainland inlets and Johnstone Strait, and exhibits physical and chemical properties quite distinct from the latter (Figs. 3, 4).

## PHYSICAL CHARACTERISTICS

### *Hydrographic Conditions in Queen Charlotte Strait*

The salinity distribution near the surface (Figs. 7–10) in Queen Charlotte Strait suggests a general circulation in a counter-clockwise fashion. The runoff from the mainland inlets along the north shore and at the east end of the Strait, particularly from Knight Inlet at the east end, contributes large volumes of fresh water which tends to move seaward at the surface, mixing as it progresses along the north shore into Queen Charlotte Sound with the deeper more saline water below. The more saline water from the open ocean and Queen Charlotte Sound moves into the Strait centrally as well as along the Vancouver I. side of the Strait and along the north side of Malcolm I. The intrusion of high salinity water along the deep channels in the central part of the Strait is also apparent. This general pattern of salinity distribution, with fluctuations to varying degrees near the surface, is pronounced in the upper zone to a depth of at least 20 m. (Figs. 7–10).

Although strong winds may assist in the movement of water near the surface there is clear evidence at times of the movement of water against the wind and there are strong tidal currents throughout the region. The cur-

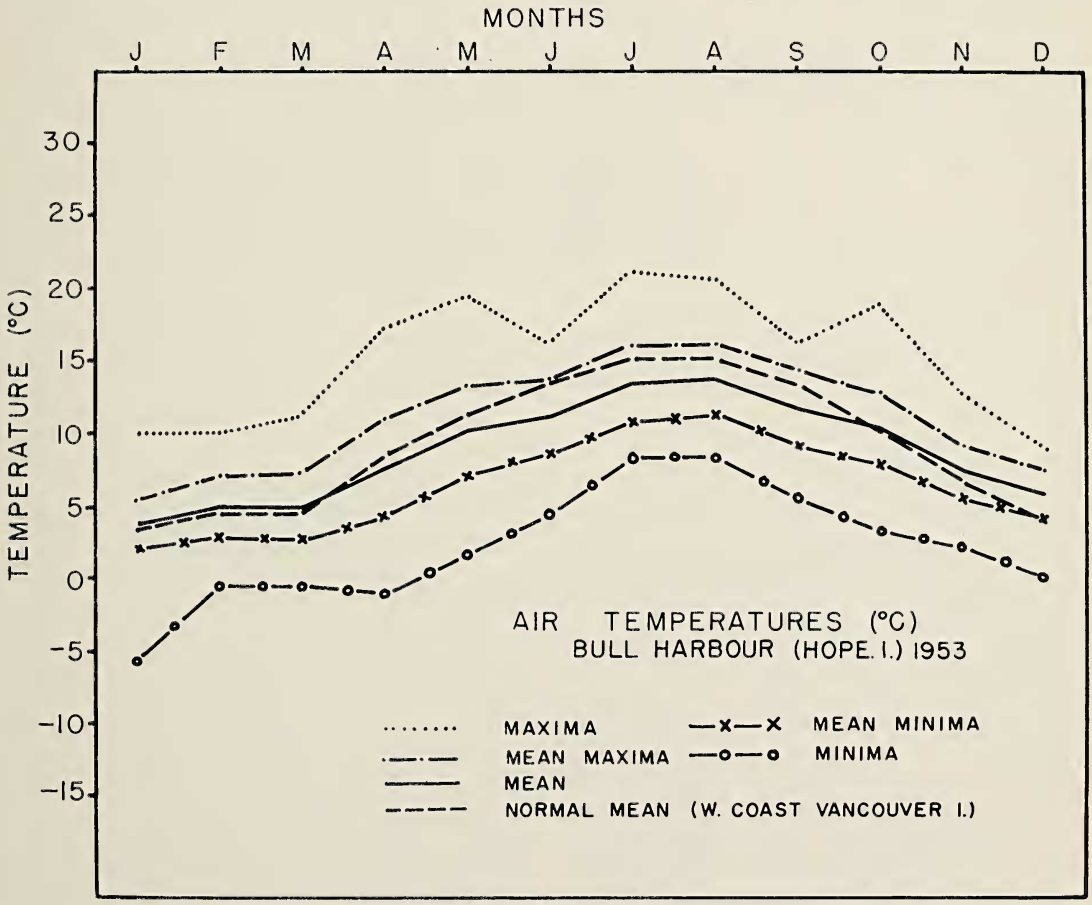


FIG. 26. Monthly air temperatures at Bull Harbour, B. C., for 1953.

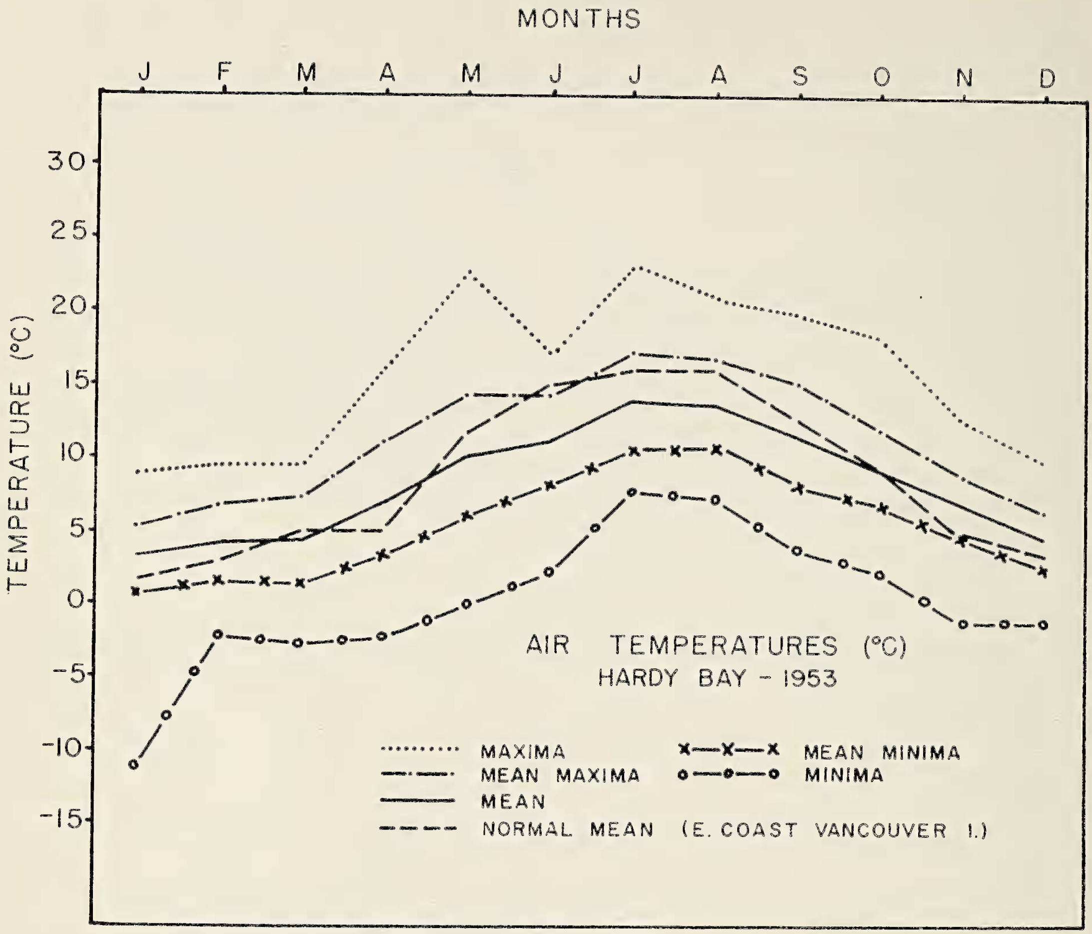


FIG. 27. Monthly air temperatures at Hardy Bay, B. C., for 1953.

rent velocities involved vary considerably but at times may reach at least 80 cm/sec from near the surface to a depth of 20 m., and in deeper portions of the Strait, although generally much less, they may attain as much as 57 cm/sec at a depth of 125 m.

An analysis of surface salinity data over a 10-year period (Fig. 11) from Pine I. Lighthouse, which is near the entrance to Queen Charlotte Strait, indicates a salinity maximum of about 33 ‰ and a minimum of about 30 ‰, with an annual mean of 31.75 ‰. Although this station is not characteristic of the Strait itself, the data available probably give a reasonable approximation of the annual salinity fluctuations for the Strait. Insufficient data are available from Pulteney Point on Malcolm I. to analyze the seasonal fluctuations more precisely in the central region of the Strait, but for the period available (Fig. 12) a range of about 28 ‰ to 32 ‰ with an annual mean of 21.50 ‰ is indicated.

Seasonal data indicate that near the surface the distribution of salinity throughout the year follows the same general pattern, decreasing toward the mainland and being higher along the Vancouver I. side of the Strait. At any one point, however, there is a general decrease in salinity in time from the maximum in April to a minimum in midsummer, when the maximum runoff from the mainland inlets occurs. The winter salinity may be somewhat modified near the surface during the period of maximum precipitation, which may reduce salinity near the surface.

The minor extent of fluctuations that occur in the salinity distribution in the upper 20 m. is indicated by data taken at a number of anchor stations (Figs. 13–17). These fluctuations are greatest at or near the surface and, in certain instances, as near the Klucksiwi River (Fig. 15), show the influence of fresh-water inflow of a more localized nature.

A comparison of the temperature–salinity characteristics of various parts of the Strait and the connecting bodies of water by means of T–S diagrams (Figs. 3, 4) indicates the discreteness of the water masses typical of Johnstone Strait, mouth of Knight Inlet, and Queen Charlotte Sound. The T–S diagrams for Queen Charlotte Strait indicate a characteristically intermediate condition between these extremes in properties of temperature and salinity for the greater part of the Strait.

An analysis of surface temperature data over a 10-year period (Fig. 18) from Pine I. Lighthouse, which is near the entrance to Queen Charlotte Strait, indicates a temperature maximum of about 12°C. and a minimum of about 5°C., with an annual mean of 8.6°C. Although this station, as already indicated, is not characteristic of the Strait itself in all respects, it probably gives a reasonable approximation of the annual temperature fluctuations. Insufficient data are available from Pulteney Point on Malcolm I. to analyze more precisely the seasonal

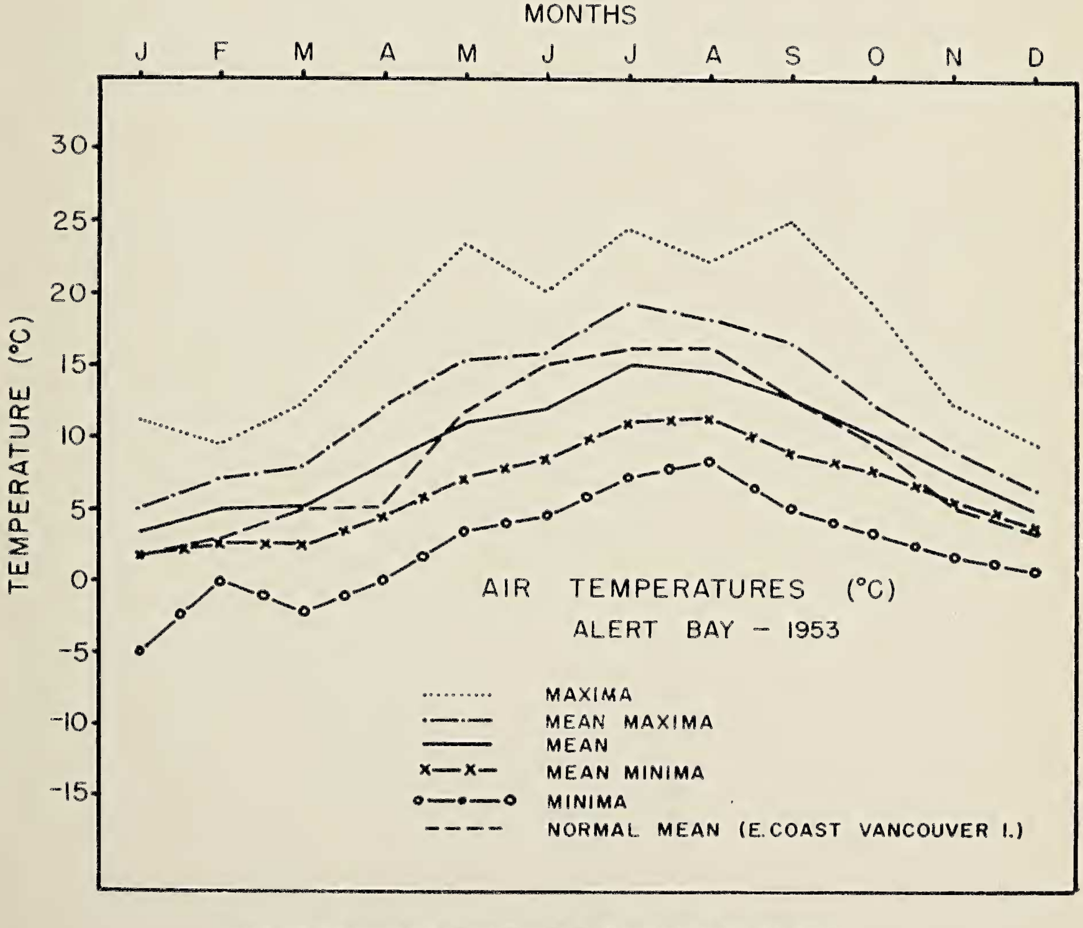


FIG. 28. Monthly air temperatures at Alert Bay, B. C., for 1953.

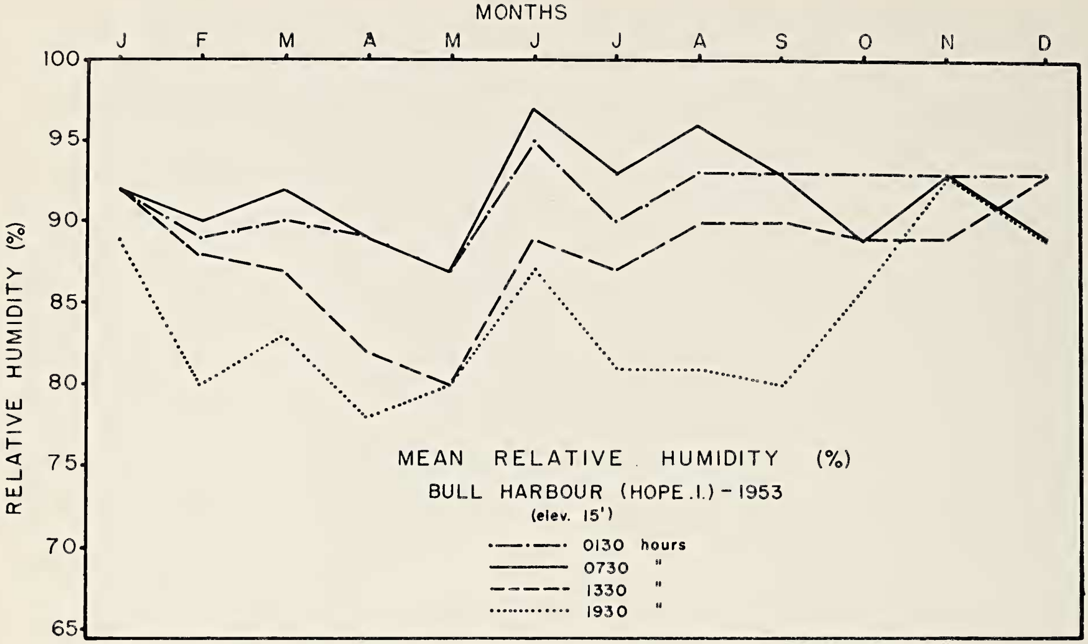


FIG. 29. Monthly relative humidity at Bull Harbour, B. C., for 1953.

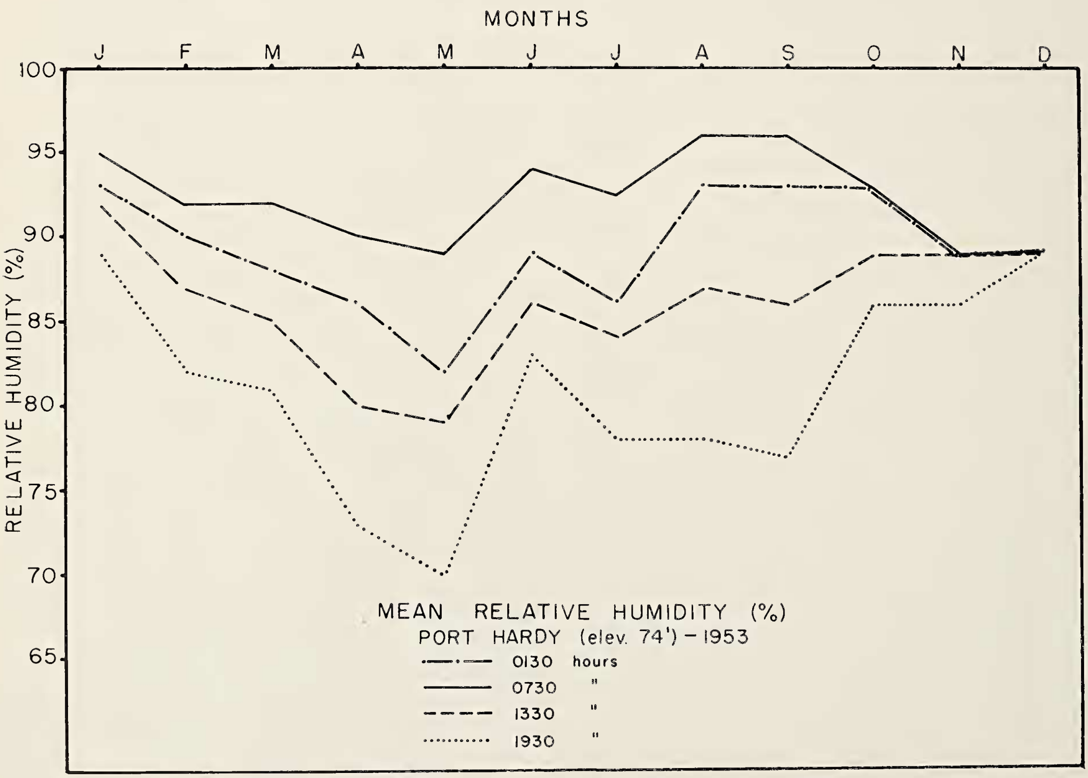


FIG. 30. Monthly relative humidity at Port Hardy, B. C., for 1953.

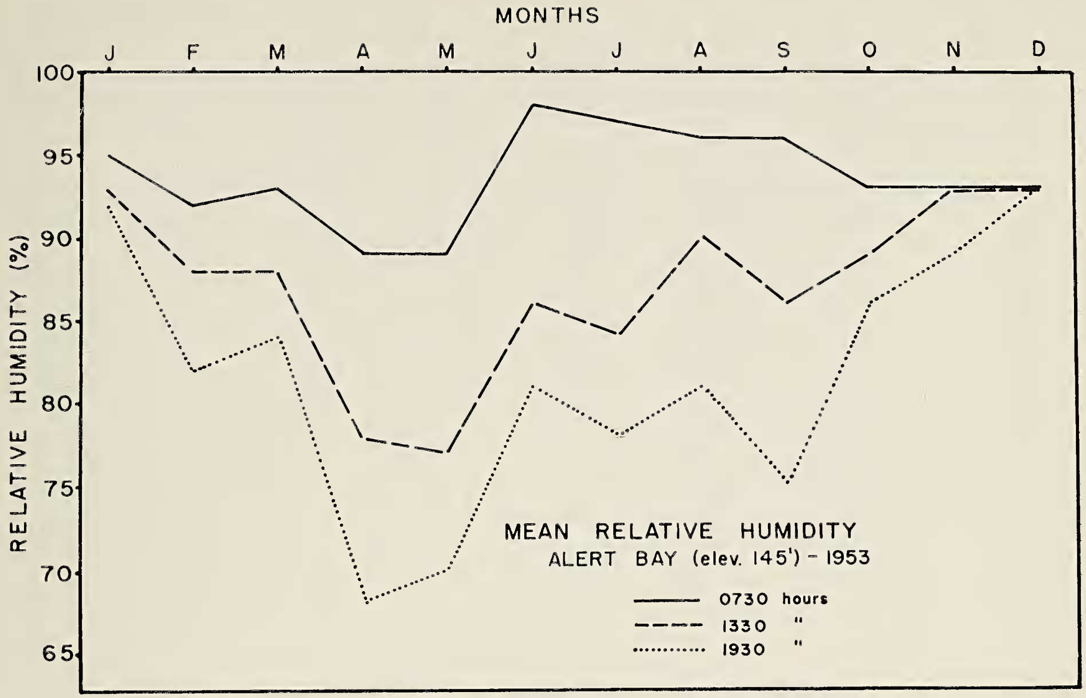


FIG. 31. Monthly relative humidity at Alert Bay, B. C., for 1953.

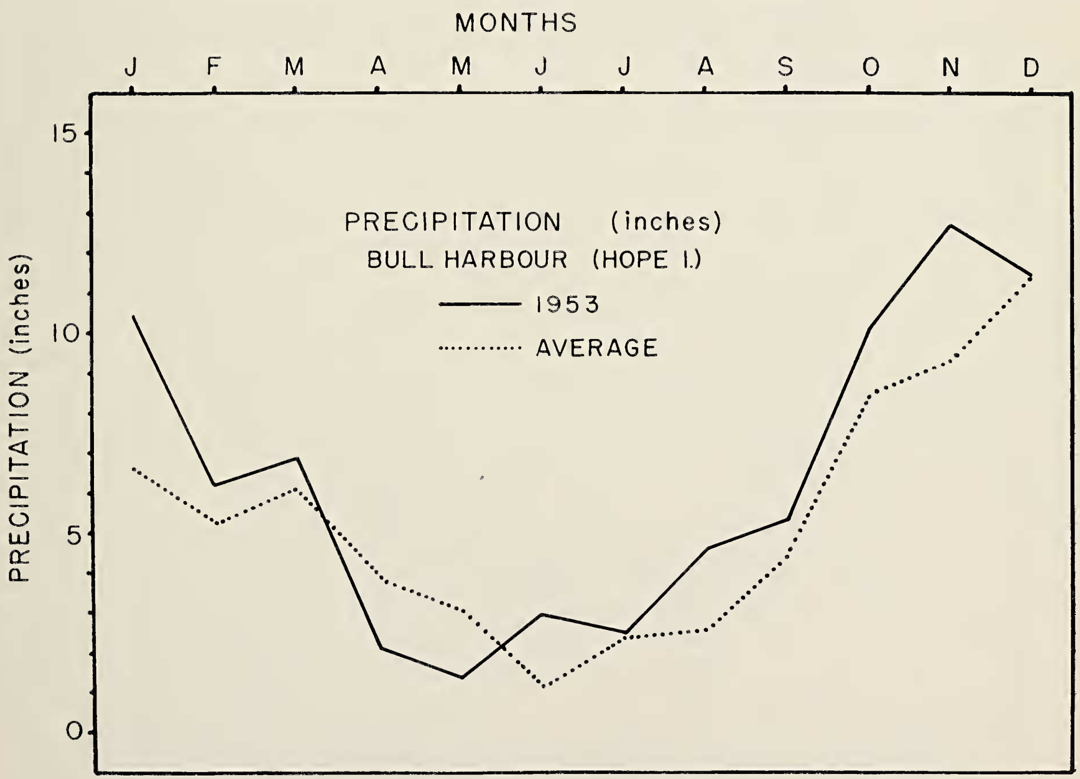


FIG. 32. Monthly precipitation at Bull Harbour, B. C., for 1953.

fluctuations in the central region of the Strait, but for the period available (Fig. 19) a range of from about 5° to 11°C. with an annual mean of 8.25°C. is indicated.

The temperature distribution with depth, as shown by bathythermograph records taken at shallow anchor stations, indicates a well-mixed region near the surface along Vancouver I. and Malcolm I. (Figs. 20–24). Except for slight anomalies the water is generally almost isothermal, with temperatures during this period of observation seldom above 11°C. at the surface and falling to not less than 8°C. at a depth of 20 m. As indicated from the anchor stations, there are no marked changes with time in this general picture of the vertical distribution of temperature, and at any one depth the fluctuations indicated were less than 2 C.° (Figs. 13–17).

However, there is a slight difference (usually not more than 1 C.°) in temperature at the surface at most times of the year, with the water along the Vancouver I. side being warmer than that along the mainland side of the Strait. This is a result of the inflow of colder, less saline water from the mainland inlets.

Seasonal data indicate that in general during the summer months the temperature at the surface is seldom above 10°C. and at a depth of 20 m. is seldom above 9°C. During the winter months it is seldom below 7.5°C. at the surface but may be about 7°C. at a depth of 20 m. This picture of the vertical temperature distribution is somewhat modified during the winter as a result of surface cooling of the water down to a depth of about 20 m. and a temperature inversion has been observed in January which disappears by April. During this early period the water at the depth of 20 m. and, in places, even to a depth of 400 m., may be warmer than that in the upper 20 m. by as much as 1 C.° and

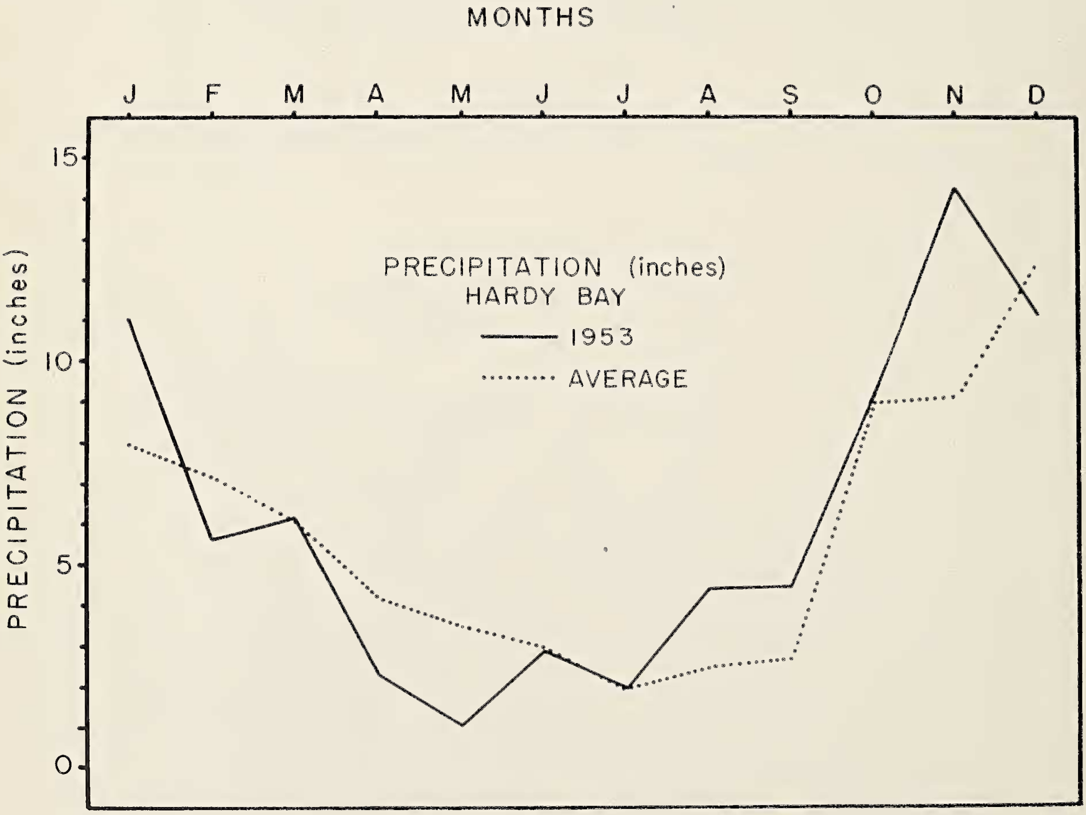


FIG. 33. Monthly precipitation at Hardy Bay, B. C., for 1953.

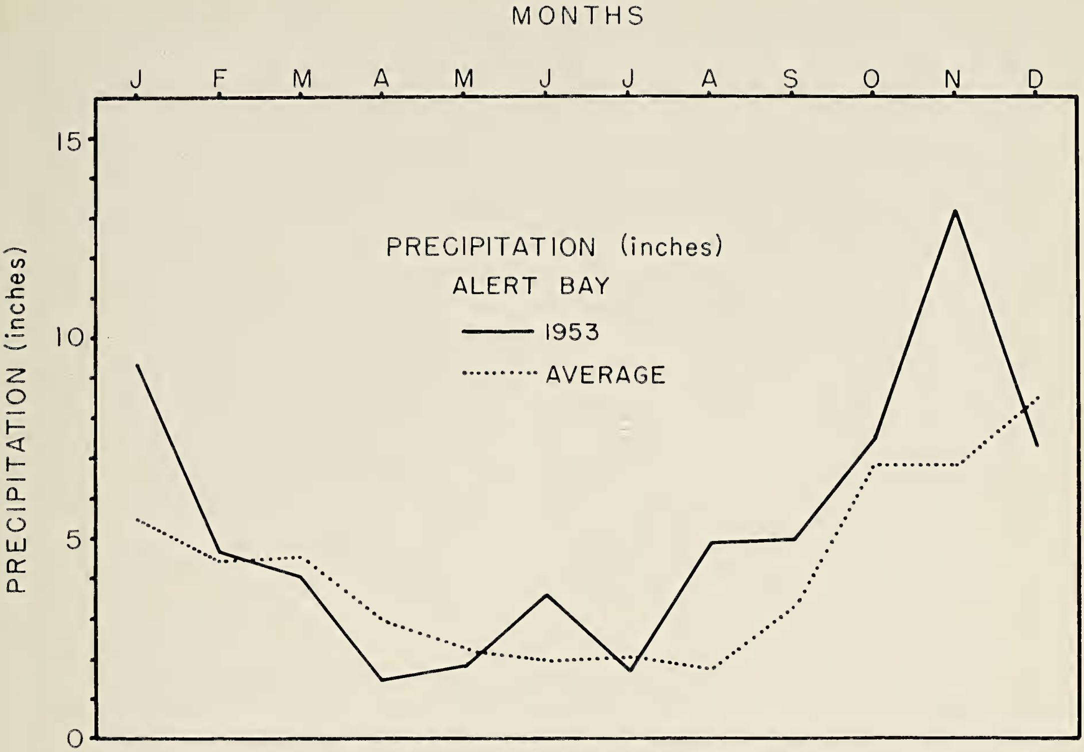


FIG. 34. Monthly precipitation at Alert Bay, B. C., for 1953.

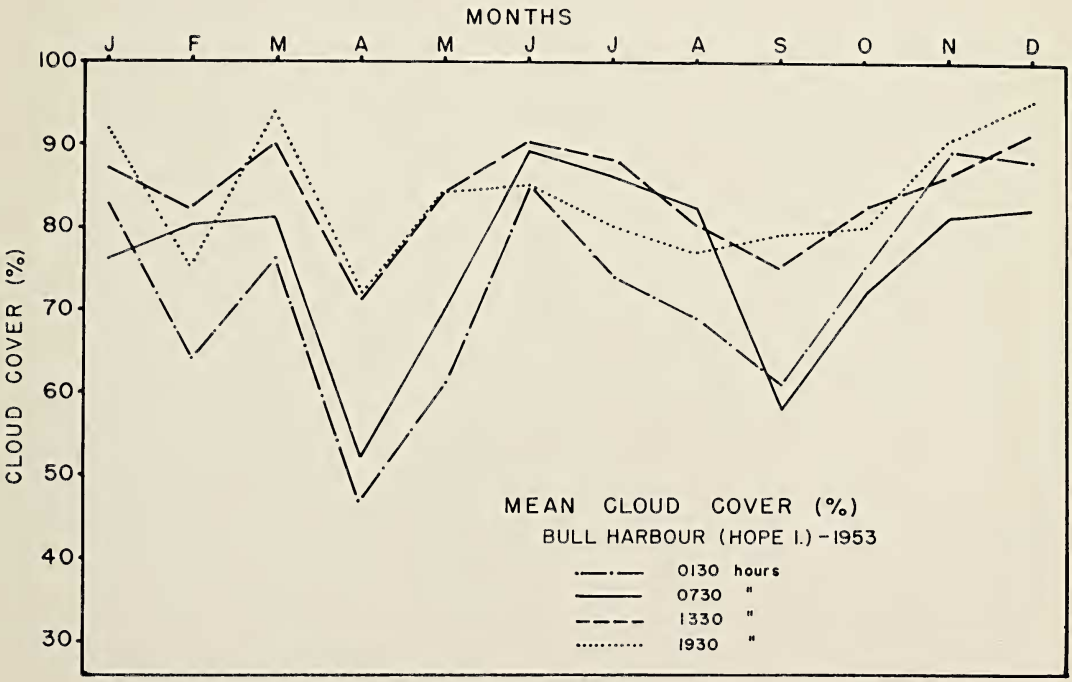


FIG. 35. Monthly cloud cover at Bull Harbour, B. C., for 1953.

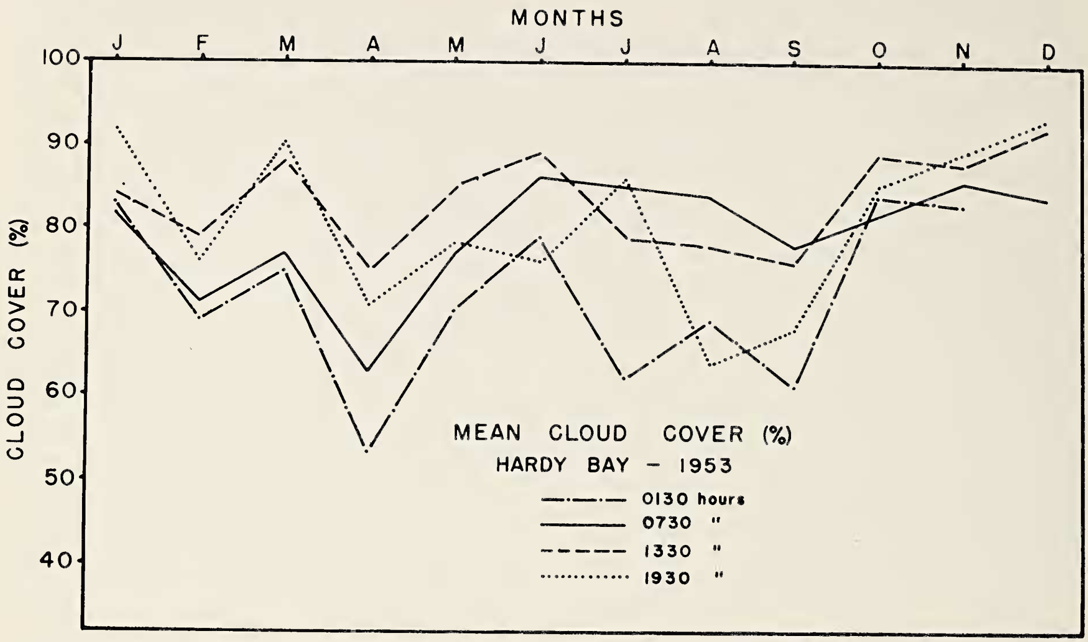


FIG. 36. Monthly cloud cover at Hardy Bay, B. C., for 1953.

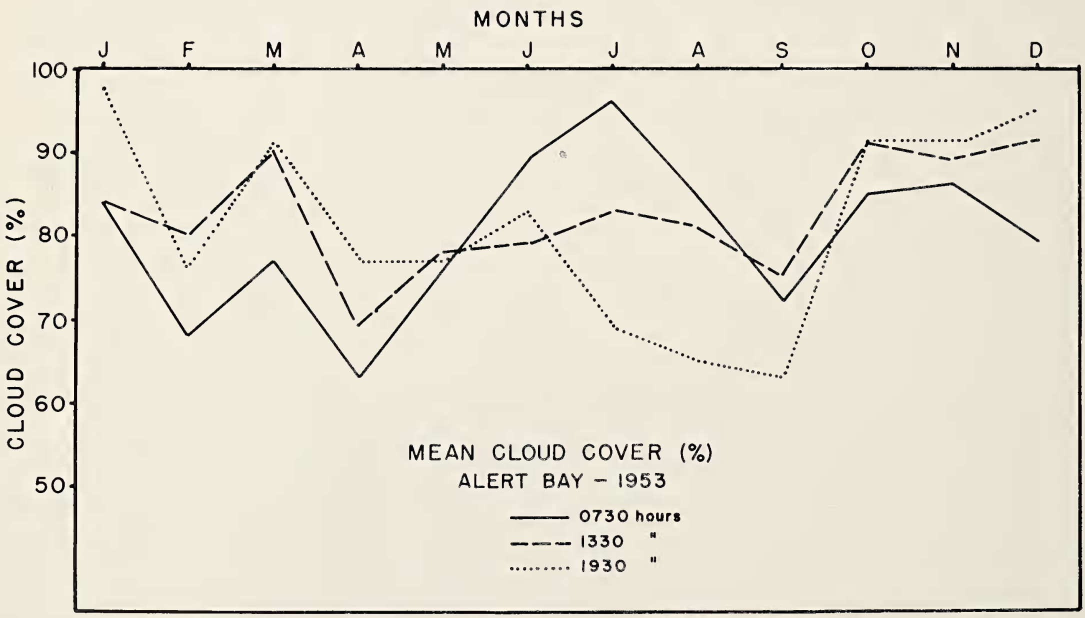


FIG. 37. Monthly cloud cover at Alert Bay, B. C., for 1953.

then fall to a lower temperature again, beneath this warmer upper layer, down to between 6° and 7°C. in the deeper regions.

Thus the environment presented to the intertidal and immediate subtidal zones (see Fig. 25 for terminology) appears to be a relatively stable one as far as the temperature of the seawater is concerned.

*Meteorological Conditions*

The intertidal region, however, during periods of exposure, is subjected to a varying degree to meteorological conditions, particularly fluctuations in temperature and precipitation, which must be considered in assessing the environment of organisms in this region. A comparison of the meteorological data (air temperatures, precipitation, mean relative humidities, and mean cloud cover) available for the coast of British Columbia, particularly from Bull Harbour (Hope I.), Hardy Bay, and Alert Bay, gives some picture of the meteorological conditions at the northeast end of Vancouver I. (Figs. 26–37).

Along the coast, air from the maritime Pacific Ocean is usually present and results in mild winters and cool summers. Holding a high moisture content, this air does not become extremely hot or cold. However, occasional outbreaks of continental air (polar) from the interior of the

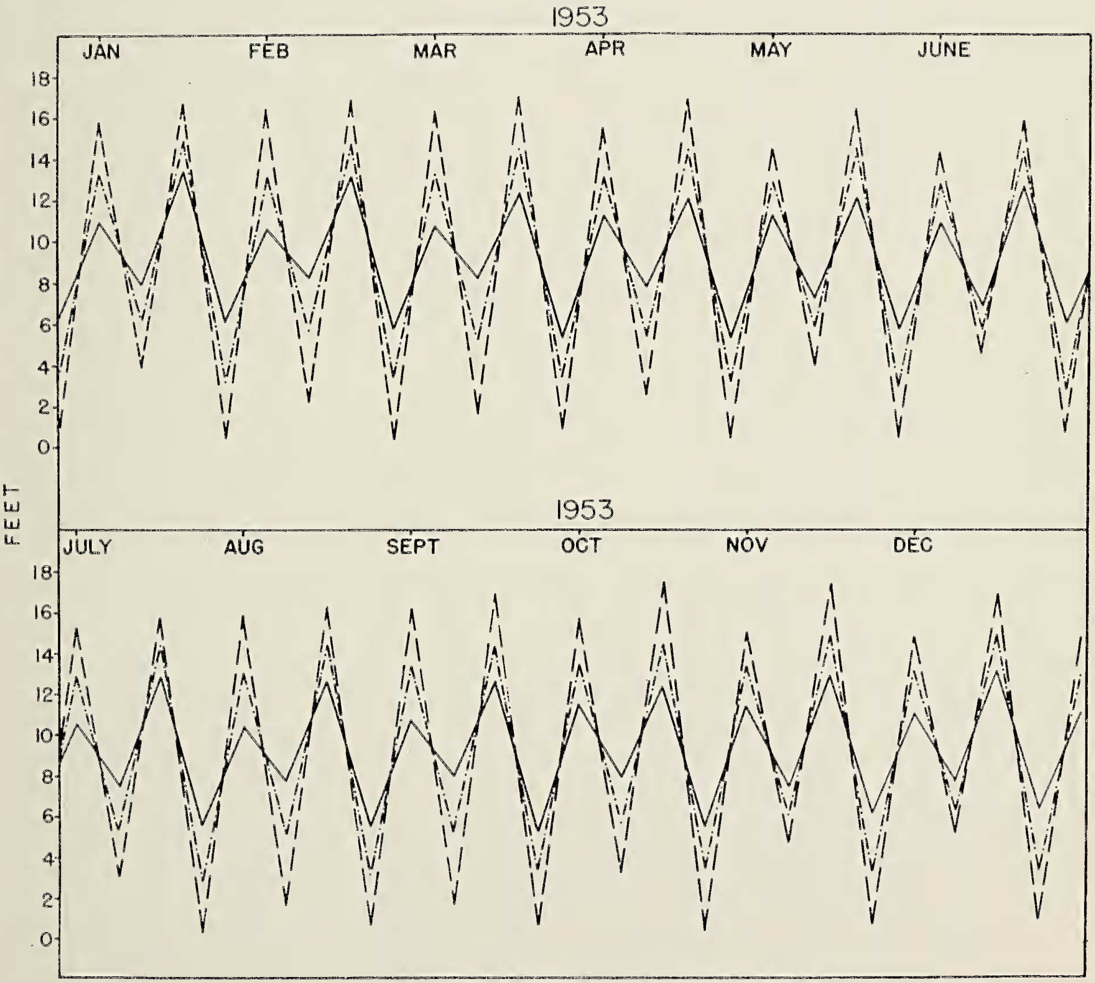


FIG. 38. Monthly summary of tidal features at Hope Island for 1953 (see Figure 39 for significance of lines).

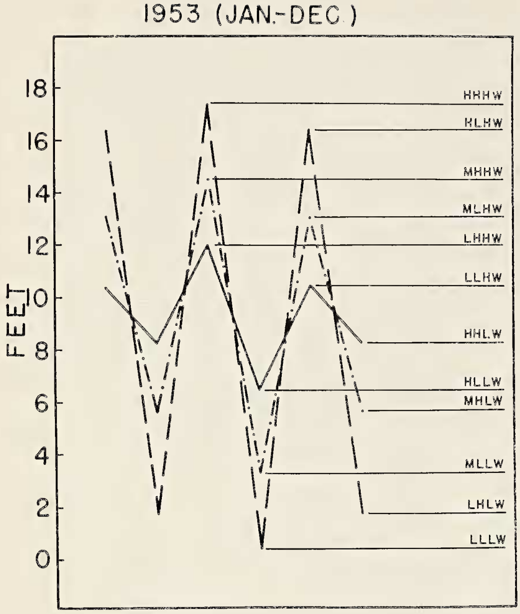


FIG. 39. Summary of tidal features for 1953.

continent bring cold periods during the winter, although generally the Coast and Cascade mountains provide considerable protection. Along the outer coast, the maritime conditions, which are present almost continually, result in high precipitation, prolonged cloudiness, and small ranges in temperature—the typical conditions prevailing in the vicinity of Hope I. (Figs. 26, 29, 32, 35) and Hardy Bay (Figs. 27, 30, 33, 36), despite the fact that these points are somewhat on the lee side of Vancouver I. Along the inner coast and the lee side of Vancouver I., where there is some protection from the maritime influence, precipitation and cloudiness are somewhat reduced and ranges in temperature are somewhat increased, as at Alert Bay (Figs. 28, 31, 34, 37).

The number of frost-free days in the whole Queen Charlotte Strait region averages 200–250 in a year. In both outer and inner regions there are no months with all temperatures ranging below 0°C. In the outer coastal region 4 to 5 months have temperatures above 10°C., and in the inner coastal region 5 to 6 months have temperatures above 10°C. In the outer coastal region, depending upon the locality, the mean monthly air temperatures for January are 1.7° to 4.4°C., and for July 13.3°C., and the mean daily temperatures are —1.1° to 1.7°C. and 15.6° to 18.9°C. for the same months, respectively. In the inner coastal region, depending upon the locality, the mean monthly air temperatures for January are 1.7° to 3.3°C., and for July 15.6° to 18.3°C., and the mean daily temperatures are —1.1° to 0°C. and 21.1° to 23.9°C., respectively, for the same months.

Although some restricted regions of British Columbia on Vancouver I. average as much as 264 in. of rain, in the Queen Charlotte Strait region the annual rainfall averages between 40 and 60 in. at the inner end (including Alert Bay and Malcolm I.), with between 5–10 per cent as snow, and between 60 and 100 in. at the outer end (including Hope I. and Port Hardy), with less than 5 per cent as snow. The period of minimum rainfall is in the summer,

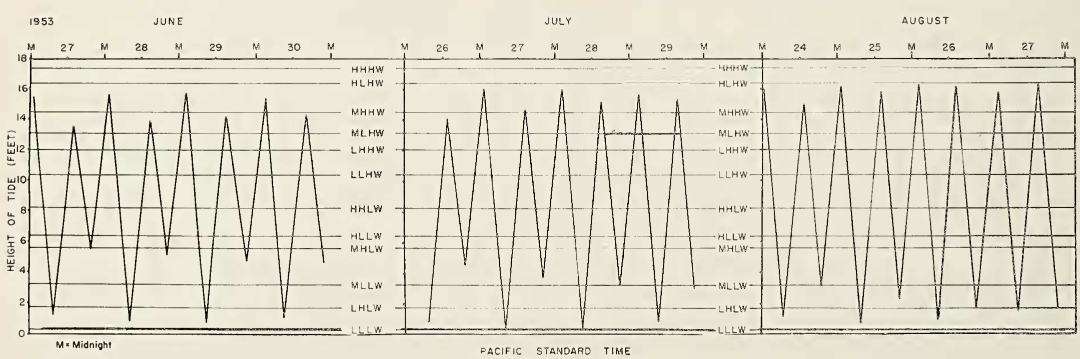


FIG. 40. Tidal features for the periods of greatest exposure during summer months of 1953.

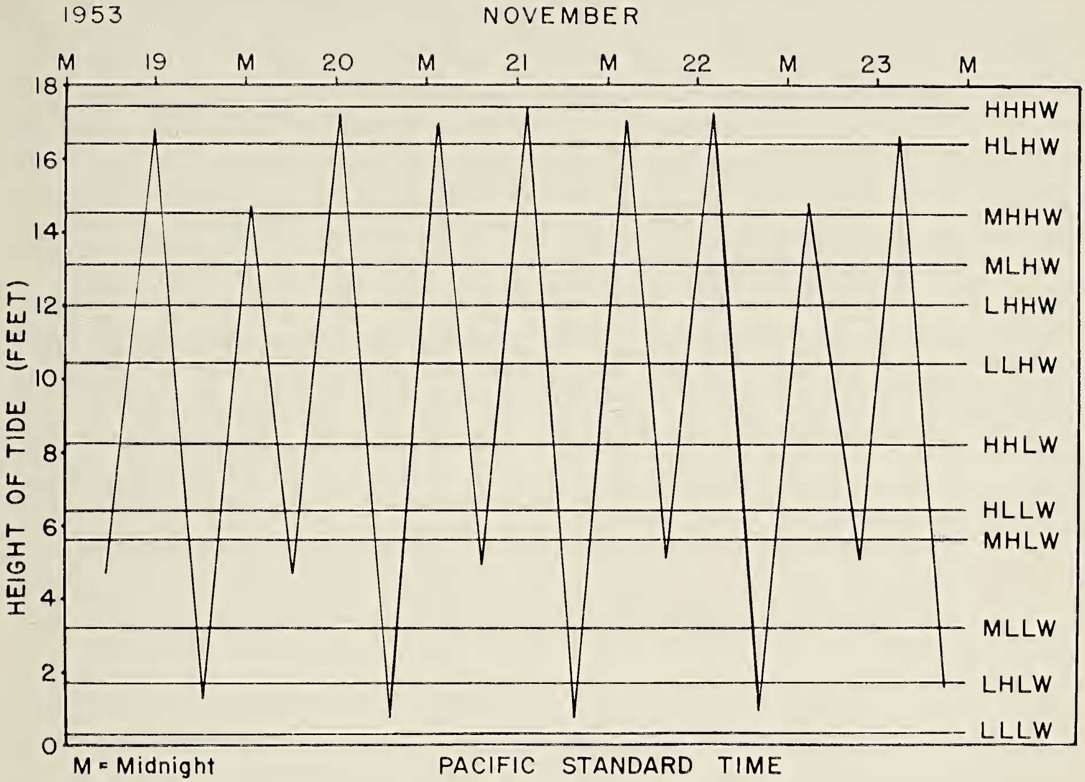


FIG. 41. Tidal features for period of greatest exposure during winter months of 1953.

with between 2–3 in. on the average falling during August in the Strait, and the maximum rainfall occurs in the winter, with between 9–13 in. on the average in December.

Near the entrance of the Strait, especially along the north side of Hope I., conditions of heavy surf generally prevail. Even when there is no sea a heavy swell is common. Farther down in the Strait to the south and east there is an area protected by scattered islands and reefs near the entrance, from the heavy swell from the open ocean, but this whole area is subject to strong westerly winds in the summer months and to even stronger southeasterly winds during the winter months, so that the Strait is generally subjected to strong wave action and wind mixing. During the period mid-September to mid-May the southeasterly winds are predominent and blow at speeds frequently up to 40 m.p.h. and occasionally higher. During the period mid-May to mid-September the westerly winds predominate and blow at speeds up to 25 m.p.h. Particularly during this latter period, however, there may be considerable calm periods, especially during the morning hours, followed by strong seas which reach a peak about 1600 hrs. and then drop rapidly to relative calm by 2000 hrs.

*Tidal Characteristics*

The tidal amplitude in the vicinity of Hope I. is usually about 17 ft. and the highest on record (37 years) was almost 19 ft. (December, 1941). An extensive intertidal flora and fauna is exposed during low tide periods in this zone. Continuous tidal data are recorded since 1949 at Alert Bay, near station 8 (Fig. 6). At the north end of Vancouver I. the tides are semidiurnal and only moderately declinational, and thus springs and neaps are distinguishable (Figs.

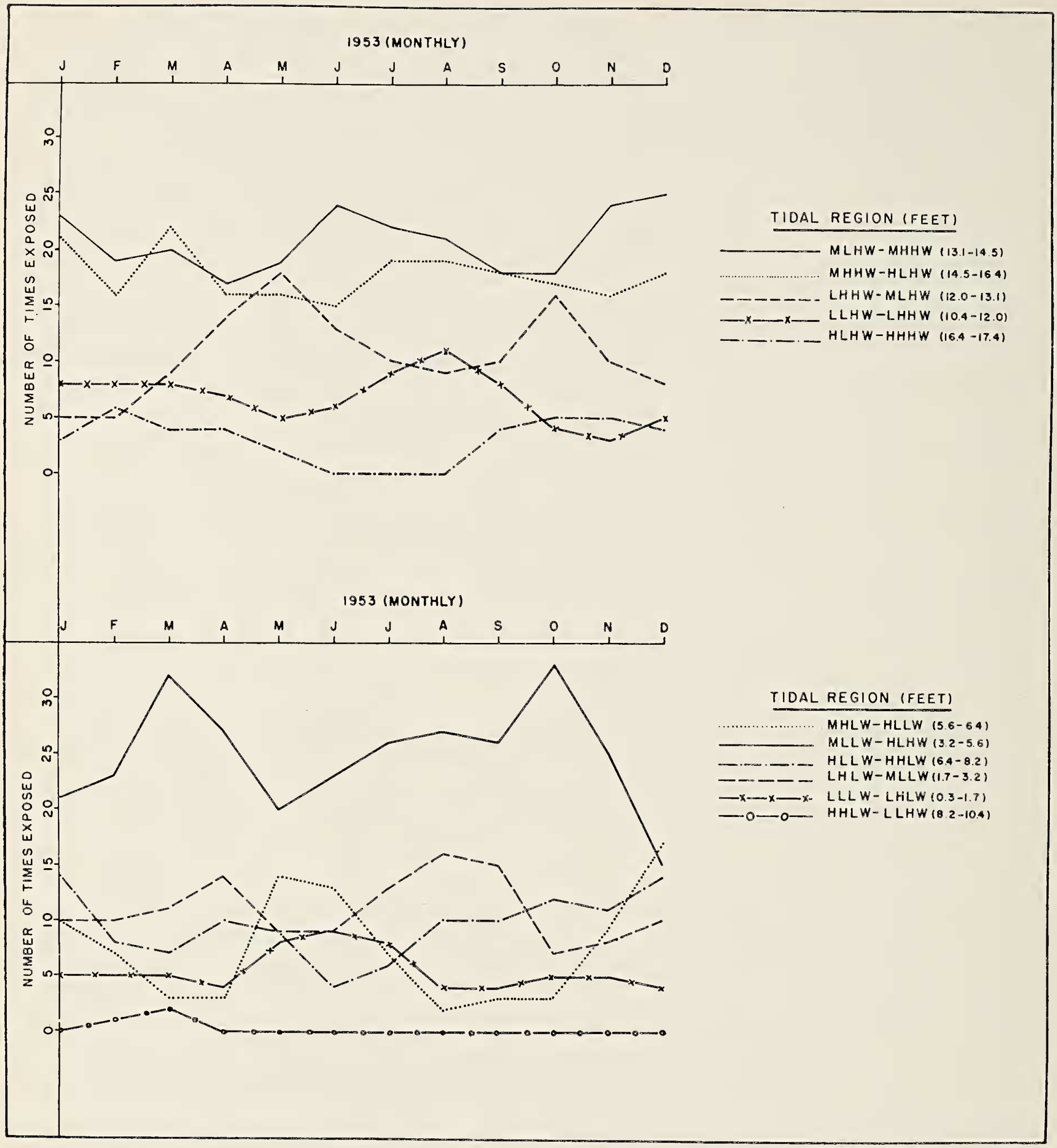


FIG. 42. Diagram showing number of times each month during 1953 various levels in the intertidal zone were exposed.

38–41). Twice a month there are two tides a day which are about equal, and in the intervals between there is a much greater inequality in the height of any two successive low waters than between the two high waters of the same day. During the summer months (Fig. 40) the lowest low waters occur during daylight hours and during the winter months (Fig. 41) the lowest low waters occur late at night or early in the morning.

The number of times during the year when each of the various levels recognized (Fig. 39) are exposed is indicated in Figure 42, and the number of days of continuous exposure of the upper portions of the intertidal zone are shown in Figure 43. The number of times (and per cent) these levels are exposed (Fig. 44) and submerged (Fig. 45) are also presented in an attempt to indicate possible critical levels. The tide levels are referred to in feet above or below the datum (zero point) which, for the coast of British Columbia, is the level of lowest normal tides.

*Chemical Characteristics*

During the summer months, when plant production is at its peak in Queen Charlotte Strait, the surface zone may be supersaturated with oxygen; values in excess of 15 mg/l are frequently encountered. The maximum values generally prevailing near the surface and to a depth of 20 m. are between 7 and 10 mg/l. During the summer months the values are somewhat higher than in the winter. The maximum concentration of oxygen occurs at a depth between 2 and 5 m. (Figs. 46, 47), rather than right at the surface during the summer, and is related to the region of maximum phytoplankton activity. The water throughout most of the Strait has a higher oxygen content near the surface (Figs. 46, 47) than in Queen Charlotte Sound or in the adjacent connecting mainland channels. Although marked fluctuations occur locally in the upper 10 m., the general picture is more stable (Figs. 13–17) at greater depth.

Phosphate concentrations ($PO_4$–P) are not available for the winter months, but for the summer, during which minimum amounts are probably reached, the values present (Fig. 48) were between 0.5 and 2.0 mg.–at. per liter in the upper 20 m. The minima were generally in the upper 10 m. and most of the minima for the Strait and Queen Charlotte Sound were between 1.0 and 1.5 mg.–at. per liter.

BIOLOGICAL CHARACTERISTICS

Biological observations, extending over the length of the coast, indicate that there is a high degree of uniformity in the populations of many benthonic plants and animals extending from the Strait of Juan de Fuca to Dixon Entrance. This would be anticipated under such relatively uniform conditions of temperature. In attempting to correlate the distribution of some of these organisms with salinity characteristics, as well as other oceanographic factors, there are several areas on the coast which could be used for purposes of this study. Although some supporting observations have been made in the Strait of Juan de Fuca and Dixon Entrance, this paper is restricted largely to a consideration of the vicinity of Queen Charlotte Strait near the north end of Vancouver I.

*Horizontal Distribution of Organisms in Queen Charlotte Strait*

Biological observations have been made throughout the area although a more intensive study and collection has been undertaken at Hope I., Deer I., and in the vicinity of the Keogh River, the Klucksiwi River, and Malcolm I. These areas present a transition from Hope I., where the highest salinities are encountered, to the north and east sides of the Strait, where lowest salinities are found, with Deer I. and Malcolm I. being intermediate between these extremes. The distributions in the Strait of the more conspicuous organisms (Table 1) observed during this study are illustrated in Figure 49. Although both the marine algae and the invertebrate animals have been observed, the emphasis in this study is on the more conspicuous marine algae.

Some organisms in the area are more cos-


FIG. 43. Diagram showing number of days various levels in the intertidal zone were subjected to continuous exposure.

TABLE 1

LIST OF THE MORE CONSPICUOUS SPECIES OF MARINE BENTHONIC ORGANISMS IN QUEEN CHARLOTTE STRAIT

1. *Polyneura latissima* (Harvey) Kylin
2. *Chthamalus dalli* Pilsbry
3. *Tegula funebralis* (Adams)
4. *Acmaea instabilis* (Gould)
5. *Balanus cariosus* (Pallas)
6. *Endocladia muricata* (Harvey) J. Agardh
7. *Gloiopeltis furcata* (Postels et Ruprecht) J. Agardh
8. *Prionitis lanceolata* Harvey
9. *Prionitis lyallii* Harvey
10. *Erythrophyllum delesserioides* J. Agardh
11. *Petrocelis franciscana* Setchell et Gardner
12. *Hildenbrandia occidentalis* Setchell
13. *Opuntiella californica* (Farlow) Kylin
14. *Plocamium pacificum* Kylin
15. *Gigartina papillata* (C. Agardh) J. G. Agardh
16. *Gigartina sitchensis* Ruprecht
17. *Iridaea cordata* (Turner) Bory
18. *Iridaea heterocarpa* Postels et Ruprecht
19. *Halosaccion glandiforme* (Gmelin) Ruprecht
20. *Rhodymenia palmata* (Linnaeus) Greville f. *palmata*
21. *Gastroclonium coulteri* (Harvey) Kylin
22. *Microcladia borealis* Ruprecht
23. *Ptilota asplenioides* (Esper) C. Agardh
24. *Ptilota californica* Ruprecht
25. *Ptilota hypnoides* Harvey
26. *Hymenena setchellii* Gardner
27. *Hymenena flabelligera* (J. Agardh) Kylin
28. *Cryptopleura ruprechtiana* (J. Agardh) Kylin
29. *Polysiphonia collinsii* Hollenberg var. *collinsii*
30. *Pterosiphonia bipinnata* (Postels et Ruprecht) Falkenberg var. *bipinnata*
31. *Laurencia spectabilis* Postels et Ruprecht
32. *Rhodomela larix* (Turner) C. Agardh
33. *Odonthalia floccosa* (Esper) Falkenberg
34. *Odonthalia washingtoniensis* Kylin
35. *Prasiola meridionalis* Setchell et Gardner
36. *Agardhiella coulteri* (Harvey) Setchell
37. *Saundersella simplex* (Saunders) Kylin
38. *Heterochordaria abietina* (Ruprecht) Setchell et Gardner
39. *Desmarestia intermedia* Postels et Ruprecht
40. *Desmarestia herbacea* Lamouroux
41. *Desmarestia media* var. *tenuis* Setchell et Gardner
42. *Desmarestia munda* Setchell et Gardner
43. *Soranthera ulvoidea* Postels et Ruprecht f. *ulvoidea*
44. *Myelophycus intestinale* Saunders
45. *Scytosiphon lomentaria* (Lyngbye) J. Agardh f. *lomentaria*
46. *Coilodesme bulligera* Stroemfelt
47. *Laminaria cuneifolia* J. Agardh f. *cuneifolia*
48. *Laminaria saccharina* (Linnaeus) Lamouroux f. *saccharina*
49. *Laminaria setchellii* Silva
50. *Pleurophycus gardneri* Setchell et Saunders
51. *Agarum fimbriatum* Harvey
52. *Agarum cribrosum* Bory
53. *Hedophyllum sessile* (C. Agardh) Setchell
    a. smooth form
    b. bullate form
54. *Postelsia palmaeformis* Ruprecht
55. *Lessoniopsis littoralis* (Farlow et Setchell) Reinke
56. *Pterygophora californica* Ruprecht
57. *Egregia menziesii* (Turner) Areschoug subsp. *menziesii*
58. *Fucus evanescens* C. Agardh f. *evanescens*
59. *Fucus gardneri* Silva f. *gardneri*
60. *Pelvetiopsis limitata* (Setchell) Gardner f. *limitata*
61. *Cystoseira geminata* C. Agardh
62. *Smithora naiadum* (Anderson) Hollenberg
63. *Porphyra perforata* J. Agardh f. *perforata*
64. *Farlowia mollis* (Harvey et Bailey) Farlow et *Setchell*
65. *Dilsea californica* (J. Agardh) O. Kuntze
66. *Gloiosiphonia californica* (Farlow) J. Agardh
67. *Nereocystis luetkeana* (Mertens) Postels et Ruprecht
68. *Macrocystis integrifolia* Bory
69. *Alaria nana* Schrader
70. *Alaria marginata* Postels et Ruprecht
71. *Alaria tenuifolia* Setchell f. *tenuifolia*
72. *Alaria valida* Kjellman et Setchell f. *valida*
73. *Bangia fuscopurpurea* (Dillwyn) Lyngbye
74. *Bossiella plumosa* (Manza) Silva
75. *Bossiella californica* (Decaisne) Silva
76. *Calliarthron regenerans* Manza
77. *Calliarthron schmittii* Manza
78. *Callithamnion pikeanum* Harvey var. *pikeanum*
79. *Callophyllis edentata* Kylin
80. *Callophyllis firma* Kylin
81. *Cladophora trichotoma* (C. Agardh) Kützing
82. *Spongomorpha coalita* (Ruprecht) Collins
83. *Codium fragile* (Suringar) Hariot
84. *Codium setchellii* Gardner
85. *Coilodesme californica* (Ruprecht) Kjellman
86. *Constantinea simplex* Setchell
87. *Constantinea subulifera* Setchell
88. *Corallina officinalis* var. *chilensis* (Harvey) Kützing
89. *Costaria costata* (Turner) Saunders
90. *Costaria mertensii* J. Agardh
91. *Cryptosiphonia woodii* J. Agardh
92. *Cumagloia andersonii* (Farlow) Setchell et Gardner
93. *Cymathere triplicata* (Postels et Ruprecht) J. Agardh
94. *Halicystis ovalis* (Lyngbye) Areschoug
95. *Pylaiella litoralis* (Lyngbye) Kjellman
96. *Leathesia difformis* (Linnaeus) Areschoug
97. *Haplogloia andersonii* (Farlow) Levring

TABLE 1 *(continued)*

| | |
|---|---|
| 98. *Ahnfeltia concinna* J. Agardh | 113. *Strongylocentrotus franciscanus* (Agassiz) |
| 99. *Rhodoglossum latissimum* J. Agardh | 114. *Mytilus edulis* Linnaeus |
| 100. *Iridaea lineare* (Setchell et Gardner) Kylin | 115. *Littorina planaxis* Phillippi |
| 101. *Ahnfeltia plicata* (Hudson) Fries | 116. *Dictyoneurum californicum* Ruprecht |
| 102. *Schizymenia pacifica* Kylin | 117. *Phyllospadix scouleri* Hooker |
| 103. *Rhodoglossum affine* (Harvey) Kylin | 118. *Zostera marina* L. var. *marina* |
| 104. *Flustrella corniculata* (Smitt) | 119. *Balanus nubilus* Darwin |
| 105. *Mytilus californianus* Conrad | 120. *Ulva latissima* L. |
| 106. *Mitella polymerus* (Sowerby) | 121. *Rhizoclonium riparium* (Roth) Harvey |
| 107. *Pisaster ochraceus* (Brandt) | 122. *Porphyrella gardneri* Smith et Hollenberg |
| 108. *Balanus glandulus* (Darwin) | 123. *Desmarestia ligulata* (Lightfoot) Lamouroux |
| 109. *Styela montereyensis* (Dall) | 124. *Amplisiphonia pacifica* Hollenberg |
| 110. *Haliotis kamtschatkana* Jones | 125. *Rhodymenia pertusa* (Postels et Ruprecht) J. Agardh |
| 111. *Strongylocentrotus drobachiensis* (Müller) | |
| 112. *Strongylocentrotus purpuratus* (Stimpson) | 126. *Pterochondria woodii* (Harvey) Hollenberg |

mopolitan in their distribution, particularly in their tolerance to extreme dilution. Extending throughout the Strait (Fig. 49) are forms such as *Alaria tenuifolia* Setchell f. *tenuifolia, Cymathere triplicata* (P. and R.) J. Ag., *Costaria costata* (Turn.) Saunders, *C. mertensii* J. Ag., *Laminaria saccharina* (L.) Lamour. f. *saccharina, Nereocystis luetkeana* (Mert.) P. and R., *Porphyra perforata* J. Ag. f. *perforata, Rhodomela larix* (Turn.) C. Ag., *Odonthalia floccosa* (Esper) Falk., *Mytilus edulis* Linnaeus, *Littorina planaxis* Philippi, and *Strongylocentrotus drobachiensis* (Müller).

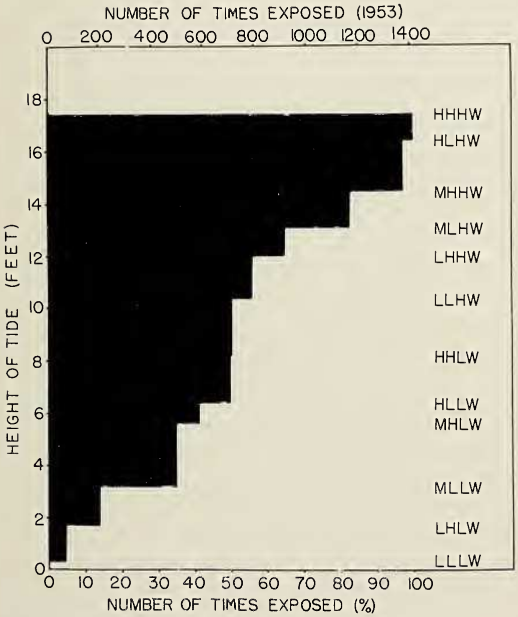


FIG. 44. Diagram showing number (and per cent) of times tidal condition caused exposure of various regions in the intertidal zone.

Restricted to the region of highest salinity, as at Hope I., are *Postelsia palmaeformis* Rupr., *Lessoniopsis littoralis* (Farl. and Setch.) Reinke, *Laminaria setchellii* Silva, *Pelvetiopsis limitata* (Setchell) Gardner f. *limitata, Dilsea californica* (J. Ag.) O. Kuntze, *Erythrophyllum delesserioides* J. Ag., *Iridaea lineare* (S. and G.) Kylin, *Hymenena setchellii* Gardner, *Ptilota asplenioides* (Esper) C. Ag., *P. californica* Rupr., *P. hypnoides* Harvey, *Mitella polymerus* (Sowerby), and *Flustrella corniculata* (Smitt).

A smooth form of *Hedophyllum sessile* (C. Ag.) Setch., *Pleurophycus gardneri* Setch. and Gardner, and *Styela montereyensis* Dall are also present in regions of highest salinity, but are somewhat less restricted in their distribution and extend into the Strait as far as Deer I.

A few organisms extend still farther into the Strait but only slightly beyond Deer I. Among these are *Alaria nana* Schrader and *A. marginata* P. and R. Still others extend from Hope I. throughout the Deer I. region and as far as Malcolm I., but not as far as the east and north sides of the Strait. Among these are *Mytilus californianus* Conrad, *Strongylocentrotus purpuratus* (Stimpson), *Macrocystis integrifolia* Bory, *Egregia menziesii* (Turner) Aresch. subsp. *menziesii*, the typical bullate form of *Hedophyllum sessile* (C. Ag.) Setch., *Alaria valida*

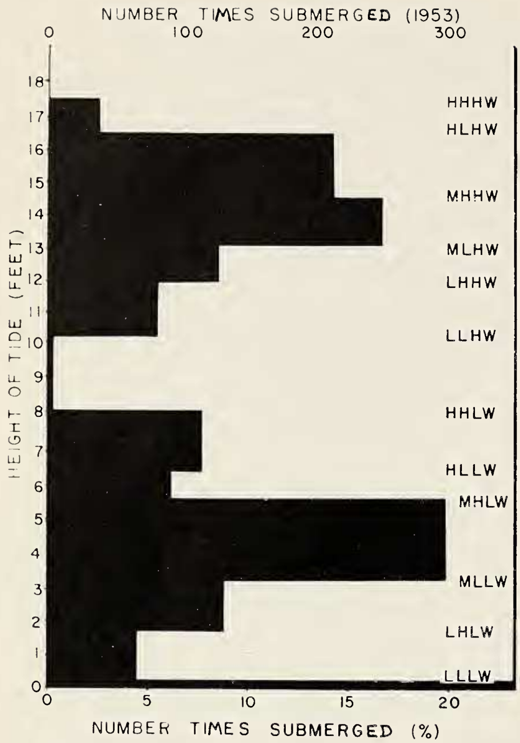


FIG. 45. Diagram showing number (and per cent) of times tidal condition caused submergence of various regions in the intertidal zone.

(Kjellm. and Setch.) f. *valida, Constantinea simplex* Setch., and *Haliotis kamtschatkana* Jones. Isolated populations of the abalone (*Haliotis kamtchatkana*), which have been noted farther eastward in Johnstone Strait and which may be related to local oceanographic features, present something of an anomaly in the general distribution. An exception to the general distribution described in this group is that of *Macrocystis integrifolia.* Although *Macrocystis* occurs in regions of high salinity and extends as far down the Strait as the north side of Malcolm I. and the south side of Numas I., it does not occur in the most exposed areas where *Postelsia* and *Mitella* are encountered.

## *Vertical Distribution of Organisms*

The vertical distributions with reference to tide levels, based on data obtained using an Abney level, are presented for some of the more conspicuous organisms at Hope I. (Fig. 50). Comparisons are made also for some of these (Fig. 51) at Hope I., Deer I., and near the Klucksiwi River, to indicate the effect exposure to surf has on the vertical distribution of some organisms.

By comparing the vertical distributions of organisms in Queen Charlotte Strait (Fig. 50) with tidal data presented with respect to emergence and submergence (Figs. 42–45), a number of limiting levels are fairly apparent. Near the top of the intertidal zone is a region (HHHW to HLHW) which is rarely submerged (Fig. 43) for more than a few hours on each of a few days at any period of the year and which

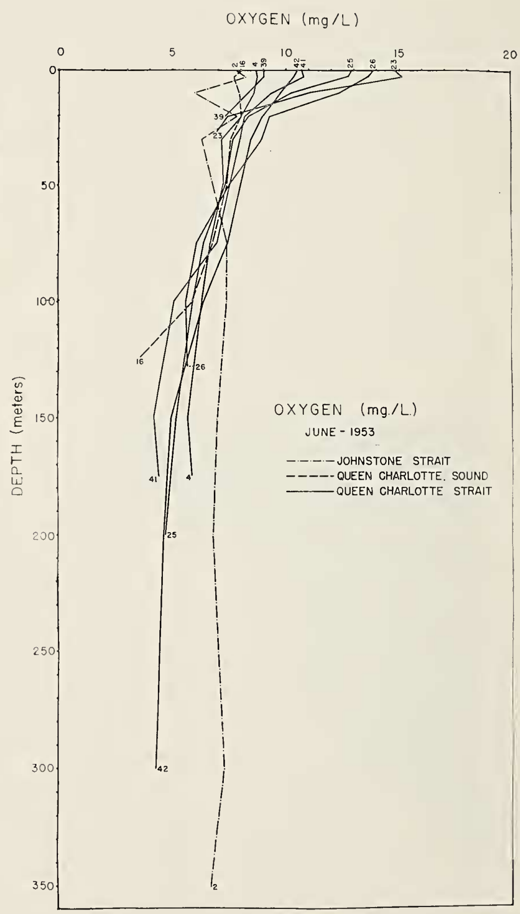


FIG. 46. Distribution of oxygen with depth at various stations in Queen Charlotte Strait and adjacent regions in June, 1953.

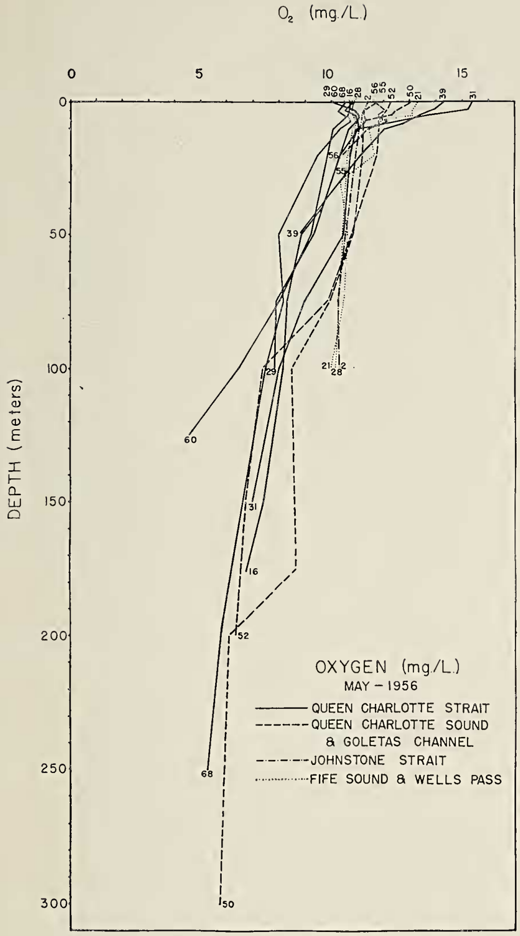


FIG. 47. Distribution of oxygen with depth at various stations in Queen Charlotte Strait and adjacent regions in May, 1956.

may be continuously exposed for as long as 4 months during the summer period. Those organisms that can tolerate such conditions are rare and in this zone one finds chiefly *Littorina,* which is capable of moving sufficiently to extend into lower less extreme zones when necessary. In the region below (HLHW to MHHW), continuous exposure to the air may last for periods ranging from a few days to almost 2 weeks, and these periods occur at least twice a month, but the rest of the time this zone is submerged at least once a day. In the region below (MHHW to MLHW), continuous exposure to the air is rarely for more than a few days at a time, and for a few months during the winter the region is submerged at least once a day. Although the upper limit of a number of the organisms (Fig. 50) in this region of the intertidal zone between 13.1 and 17.4 ft. varies to some extent with the organism, it is apparent that in this general region an upper boundary is probably determined directly or indirectly by the degree of exposure to climatic conditions. The precise tide level, if there is one, at which this boundary occurs is not clear from the data available. The effect of surf in the exposed environment may also cause some variation in the upper limit of the vertical distribution. Since the greatest change in degree of exposure within this upper region (13.1–17.4 ft.) occurs between MLHW and MHHW, a critical level is suggested at this point for a considerable number of conspicuous organisms.

All portions of the intertidal zone below MLHW are submerged at least once a day for various periods. The greatest change in conditions of submergence (Fig. 45) in the region of the middle intertidal zone (8.2–13.1 ft.) occurs between HHLW and LLHW, and it is at this point where another critical level is suggested, in some instances as the upper limit and in others as near the lower limit of the vertical distribution of certain organisms (Fig. 50).

In the lower intertidal zone (0–8.2 ft.) the most extreme change in conditions of exposure (Fig. 44) and submergence (Fig. 45) occurs between MLLW and MHLW, and this is again reflected both at the upper and lower limits in the vertical distribution of certain organisms (Fig. 50). Another critical level (Fig. 50) occurs in the region between LLLW and LHLW, where another region of marked change (Fig. 45) exists in conditions of submergence.

Although the upper limits in most instances appear to be relatively sharp, there is less consistency in this respect concerning lower limits. This suggests that other factors, perhaps competition for space or predation, may be responsible for limiting distribution, particularly downward in some instances.

## DISCUSSION

Knowing as we do from experimental work the responses of some organisms to environmental factors, it seems reasonable to anticipate

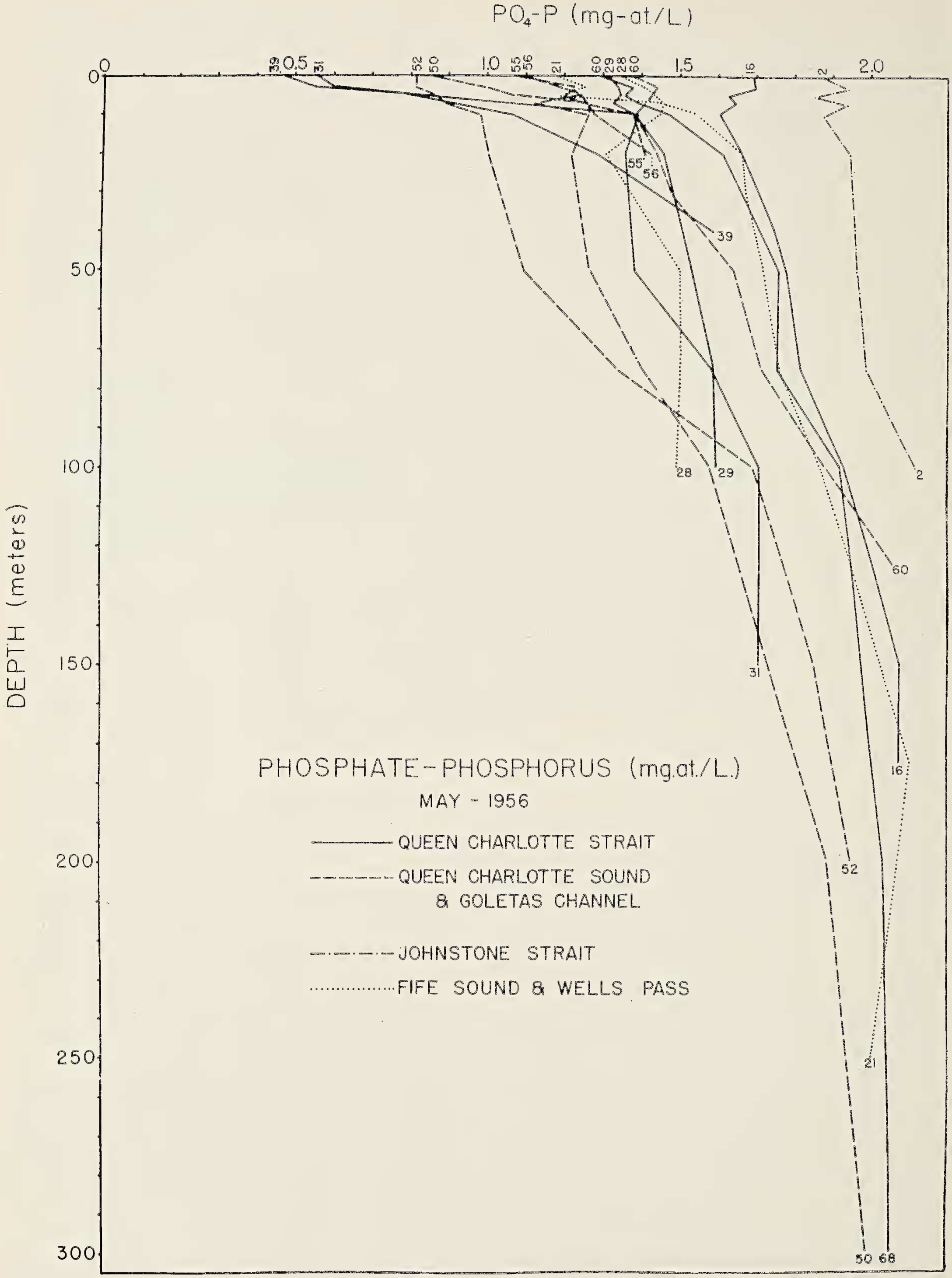


FIG. 48. Distribution with depth of phosphate-phosphorous at various stations in Queen Charlotte Strait and adjacent regions in May, 1956.

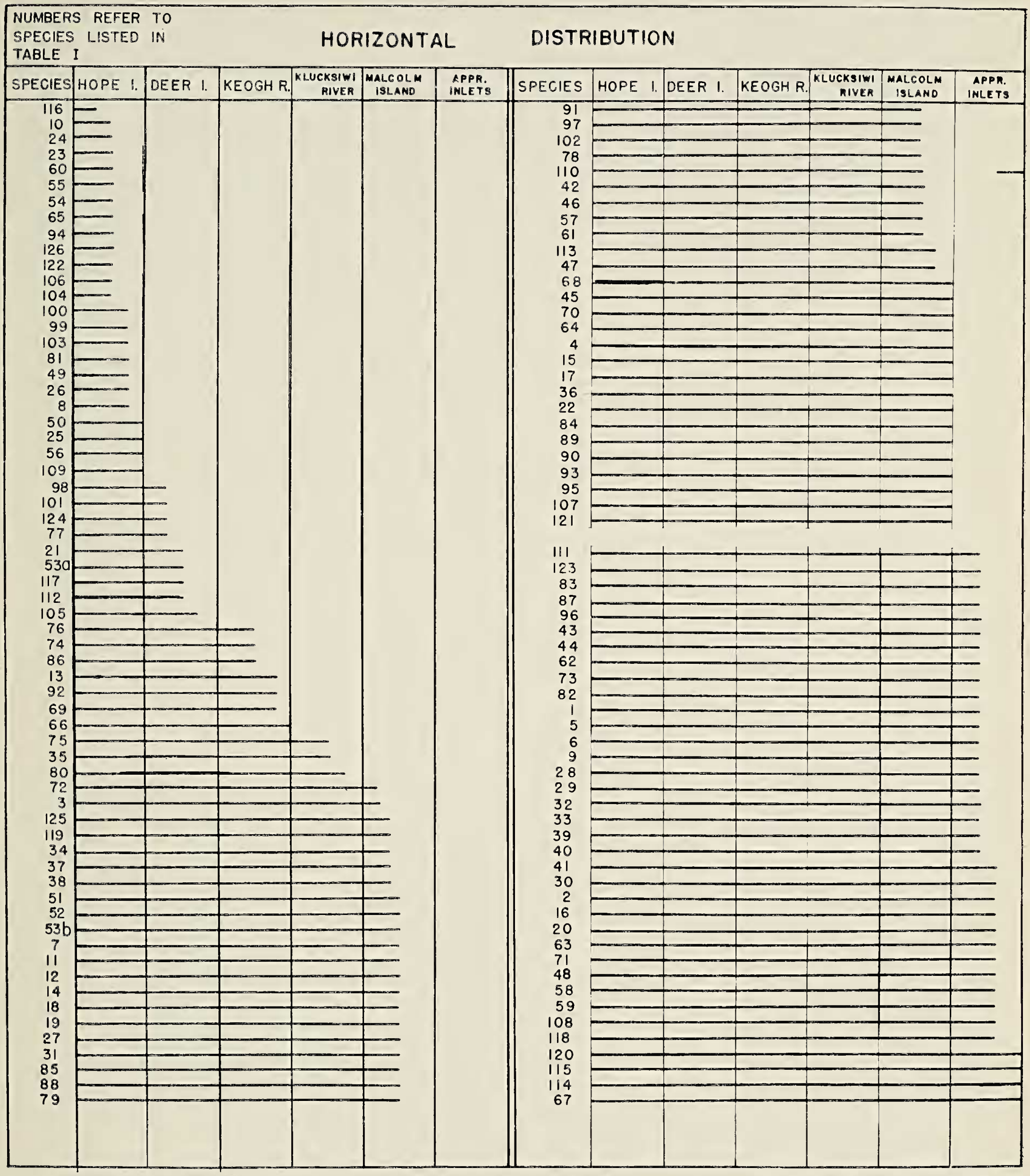


FIG. 49. Horizontal distribution of marine benthonic organisms in Queen Charlotte Strait.

that the distribution of marine organisms in time and space can be explained on the basis of oceanographic features—provided the geological, physical, chemical, and biological factors of the environment and their interaction can be adequately assessed. Any attempt to oversimplify such a many-sided and complicated study would be an avoidance of reality. However, in such a study one expects to make assumptions based on the knowledge available, in some instances of necessity by extrapolation, and to pass through a descriptive phase in an attempt to correlate observed distributions on the basis of and in relation to other factors in the environment. These comparisons may be largely qualitative in the first instance, but the intent is that they be not only qualitative but also quantitative in the final analysis and, as in all branches of science, eventually permit predictions. At best, however, only a descriptive treatment can be attempted at this point and can only point the way to further studies and hypotheses.

There have been many attempts to describe the zonation of marine organisms on the shore, and a great jumble of appalling confusion in ecological terminology has evolved to the point where some magic significance is sometimes associated with the terms and units involved. Although the need for this descriptive phase of the study (with a minimum of terminology) is recognized at an early stage of study or in a new area under investigation, once it has served

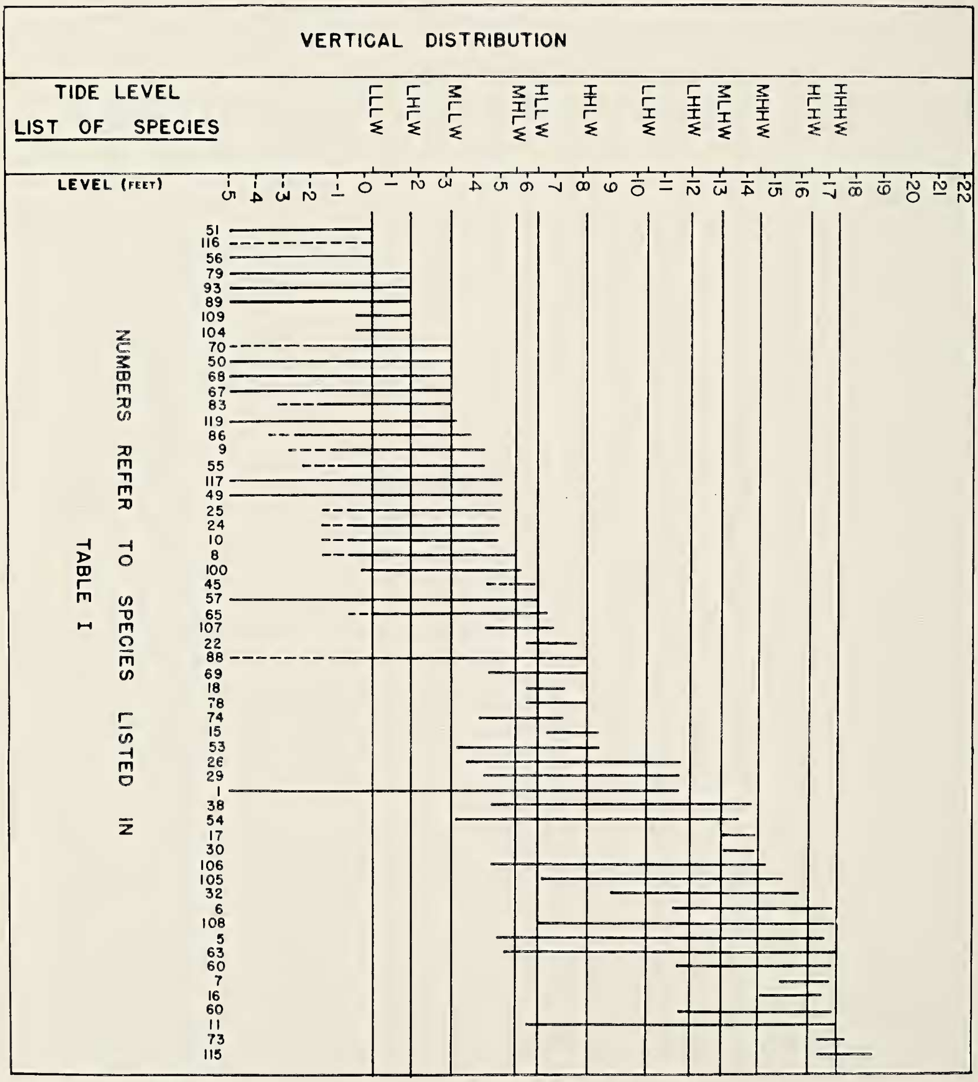


FIG. 50. Vertical distribution of some marine benthonic organisms at Hope Island.

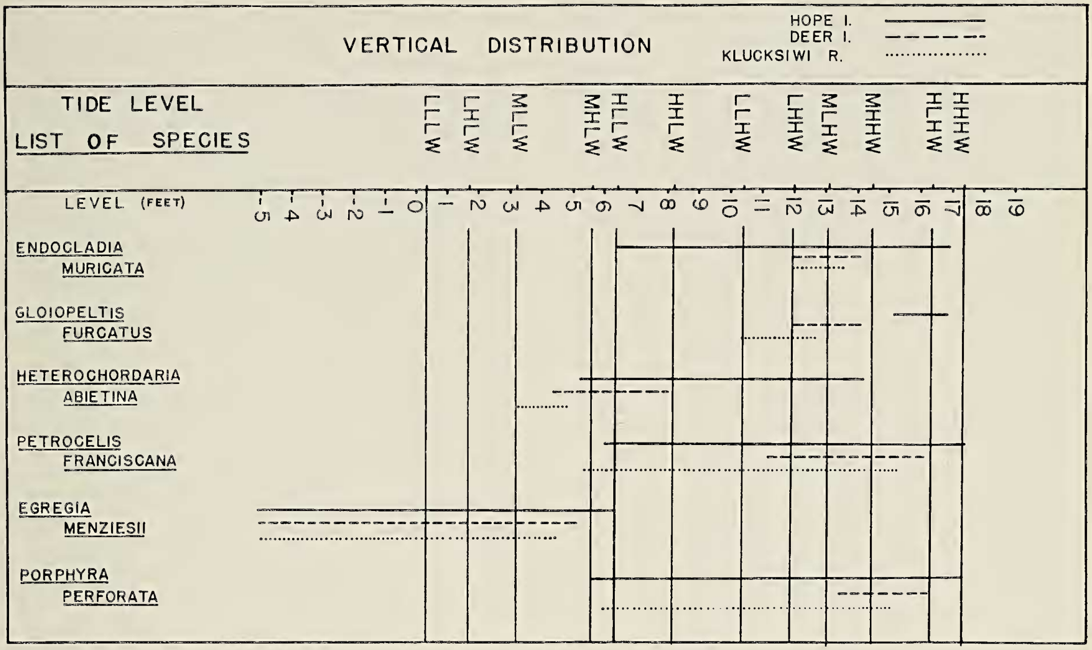


FIG. 51. Comparison of vertical distribution of some benthonic organisms at several points in Queen Charlotte Strait.

its initial purpose little refinement in this method of approach seems conducive to an explanation of the causal factors. From this point it becomes necessary to look at the problem from a new perspective involving a detailed study of the organisms concerned—an understanding of their life histories, rate of growth, reproduction, and various physiological requirements and tolerances in relation to the environment. These problems may be and, as already indicated, have been approached to some extent by actual field studies and experiments as well as by laboratory studies under controlled conditions.

It is with this philosophy in mind that this study has been approached to the extent possible from the existing data, initially from the standpoint of the oceanographer with an analysis of the environmental factors and their relation to the organisms. The success of these preliminary efforts both in the field as well as in the laboratory supports the conviction that the approach is a useful and instructive one. Differences which sometimes appear striking or significant on a broad scale are frequently less apparent and confused in a local area. The distribution of the genus *Macrocystis* is an interesting case in point. Although the global pattern of distribution of this genus is rather clearly established (Setchell, 1932; Womersley, 1954) on the basis of temperature distributions and hence follows the pattern of distribution of some of the cold water currents of both southern and northern hemispheres, the distribution of *M. integrifolia* in British Columbia follows a distinct salinity distribution. As yet, however, it cannot be conclusively stated in the latter instance that salinity itself is the causal factor. It still remains to be established whether salinity in terms of an osmotic relationship, or some parallel factor associated with open ocean water of high salinity, provides a causal mechanism for the distribution of *M. integrifolia* on this coast.

It is clear that there is a horizontal distribution of organisms, including *Macrocystis integrifolia,* in Queen Charlotte Strait which follows closely the pattern of salinity distribution in the

Strait. In turn this reflects the circulation within the area. It would be premature to say that salinity is directly responsible for the observed distributions of all the organisms encountered. But one may say that the distribution reflects the dependence on high salinity water which is characteristic of the open ocean and exposure. In some instances it may be salinity that is a direct causal factor. On the other hand, the open coast has organisms associated with surf conditions. It has been suggested that the high oxygen requirement of certain organisms is met only in such an exposed environment. However, the distributions and concentrations of oxygen in the sea in this area do not directly support this argument. The oxygen content of the waters within the sheltered Strait is as high or higher than in the surf in the exposed regions. This is particularly true in the central part of the Strait when there is a heavy bloom of phytoplankton, at which time the water may be supersaturated with oxygen to as much as 175 per cent. Likewise, although it is known that many marine algae have a high inorganic phosphate requirement, there is no evidence that this nutrient is ever limiting in this area within the zone occupied by the benthonic algae. There is a great need for further knowledge of the presence, distribution, amounts, and availability of many more dissolved inorganic as well as organic substances and perhaps even of growth substances. There is also need for a study of the quantitative aspects of removal, the rate of removal of such substances, and precise requirements for growth and reproduction in the micro-environment of the marine benthonic algae. The restriction of certain organisms to surf conditions suggests that constant movement of water is required to provide nutrients and gases which may be rapidly exhausted from the immediate or micro-environment of the individual fixed alga, or in the case of the sessile marine invertebrates, such as *Mitella polymerus,* to provide particulate food. It may be that lowering the concentration or removal by dilution or by water movement of some toxic substances which may accumulate above a certain concentration in the micro-environment is just as significant as the availability of others.

## SUMMARY

A detailed study of the horizontal and vertical distributions of marine benthonic organisms in Queen Charlotte Strait has been limited so far to the more conspicuous algae and invertebrates encountered. The relationship of these distributions to the salinity distribution indicates that more intensive study of the flora and fauna in this area, as well as elsewhere on the coast, will provide further supporting evidence indicating not only the effect of oceanographic variables on the distribution and production of marine benthonic organisms but also the possibility of using such organisms as indicators of oceanographic conditions both in time and space. The relationship of the vertical distribution of some of the organisms to certain tide levels indicates the response of the different organisms to varying degrees of exposure and submergence.

This oceanographic approach, both qualitatively and quantitatively, has given a broad understanding of some of the possible factors which are likely to be responsible for the observed distributions. However, before there can be a clear understanding and explanation of the fundamental relationships between the organisms and their environment in this region, as well as an understanding of the interrelationships and interaction among the organisms themselves, additional field observations, field experiments, and laboratory experiments must be undertaken.

## ACKNOWLEDGMENTS

Financial assistance provided by the Defence Research Board of Canada in support of this research (DRB 9520-14) over a period of several years is gratefully acknowledged. The author would also like to thank the Defence Research Board for its assistance in providing ship transportation through the Pacific Naval Laboratory, Esquimalt, and the Royal Canadian Navy for the purpose of collecting data on several cruises. In addition, assistance provided by the National Research Council, the Joint Committee on Oceanography, the Fisheries Research Board of Canada, and the University of British Columbia is gratefully acknowledged.

## REFERENCES


ANON. 1944. Observations of Sea Water Temperature and Salinity on the Pacific Coast of Canada. Fish. Res. Bd. Can., Nanaimo. Pacif. Oceanogr. Group. Vol. 5, 1942, 1943.

——— 1946. Observations of Sea Water Temperature and Salinity on the Pacific Coast of Canada. Fish. Res. Bd. Can., Nanaimo. Pacif. Oceanogr. Group. Vol. 6, 1944, 1945.

——— 1947. A Report on the Location of Marine Plants of Economic Importance in British Columbia Coastal Waters, Part 1. Brit. Columbia Res. Council Tech. Bull. 4. 5 pp., 8 figs.

——— 1948*a*. Marine Plants of Economic Importance in British Columbia Coastal Waters, Part 2. Brit. Columbia Res. Council Tech. Bull. 10. 9 pp., 9 figs., 7 tables.

——— 1948*b*. Observations of Sea Water Temperature and Salinity on the Pacific Coast of Canada. Fish. Res. Bd. Can., Nanaimo. Pacif. Oceanogr. Group. Vol. 7, 1946, 1947.

——— 1949. Observations of Sea Water Temperature and Salinity on the Pacific Coast of Canada. Fish. Res. Bd. Can., Nanaimo. Pacif. Oceanogr. Group. Vol. 8, 1948.

——— 1950. Observations of Sea Water Temperature and Salinity on the Pacific Coast of Canada. Fish. Res. Bd. Can., Nanaimo. Pacif. Oceanogr. Group. Vol. 9, 1949.

——— 1951. Observations of Sea Water Temperature and Salinity on the Pacific Coast of Canada. Fish. Res. Bd. Can., Nanaimo. Pacif. Oceanogr. Group. Vol. 10, 1950.

——— 1952*a*. Tide Tables for the Pacific Coast of Canada, 1953. Surveys and Mapping Branch, Dept. Mines and Tech. Surveys, Ottawa.

——— 1952*b*. Observations of Sea Water Temperature and Salinity on the Pacific Coast of Canada. Fish. Res. Bd. of Can., Nanaimo. Pacif. Oceanogr. Group. Vol. 11, 1952.

——— 1953*a*. Observations of Sea Water Temperature and Salinity on the Pacific Coast of Canada. Fish. Res. Bd. of Can., Nanaimo. Pacif. Oceanogr. Group. Vol. 12, 1952.

——— 1953*b*. Monthly Record Meteorological Observations in Canada, January–December, 1953. Dept. Transport Meteorological Div., Ottawa.

——— 1954. British Columbia Inlet cruises, 1953. Inst. Oceanogr. Univ. Brit. Columbia Data Rept. 3. 27 pp.

——— 1955*a*. C.G.M.V. "Cancolim II" Survey of British Columbia Coast, 1953. Inst. Oceanogr. Univ. Brit. Columbia Data Rept. 4. 72 pp.

——— 1955*b*. Data Record, Current Measurements, Hecate Project, 1954. Joint Comm. Oceanogr., 1955, Canada. 74 pp.

——— 1955*c*. Observations of Sea Water Temperature and Salinity on the Pacific Coast of Canada. Fish. Res. Bd. Can., Nanaimo. Pacif. Oceanogr. Group. Vol. 14, 1954.

——— 1955*d*. Physical and Chemical Data Record, Hecate Project, 1954, Queen Charlotte Sound, Hecate Strait, Dixon Entrance. Joint Comm. Oceanogr., 1955, Canada. 99 pp.

——— 1955*e*. Physical and Chemical Data Record, Hecate Project, with Appendix 1, Current Observations, 1955, Queen Charlotte Sound, Hecate Strait, Dixon Entrance. Joint Comm. Oceanogr., 1955. 107 pp.

——— 1956*a*. Queen Charlotte Strait, 1956. Inst. Oceanogr. Univ. Brit. Columbia Data Rept. 9. 20 pp.

——— 1956*b*. Physical and Chemical Data Record, Dixon Entrance, Hecate Strait, Queen Charlotte Sound, 1934, 1937, 1938, 1951. Joint Comm. Oceanogr., 1956, Canada. 56 pp.

——— 1956*c*. Observations of Sea Water Temperature and Salinity on the Pacific Coast of Canada. Fish. Res. Bd. Can., Nanaimo. Pacif. Oceanogr. Group. Vol. 15, 1955.

——— 1958. Indian Arm Cruises, 1957; Queen Charlotte cruise, 1957. Inst. Oceanogr. Univ. Brit. Columbia Data Rept. 12. 35 pp.

BERQUIST, P. L. 1959. A statistical approach to the ecology of *Hormosira banksii*. Bot. Mar. 1(1/2): 22–53, 23 figs., 11 tables.

BOSTOCK, H. S. 1948. Physiography of the Canadian Cordillera, with Special Reference to the Area North of the Fifty-fifth Parallel. Can. Dept. Mines and Resources Geol. Survey Mem. 247. ix + 106 pp., 31 pls., 1 fig.

CHAPMAN, V. J. 1946. Marine algal ecology. Bot. Rev. 12: 628–672.

——— 1950. The marine algal communities of Stanmore Bay, New Zealand. Studies in intertidal zonation, 1. Pacif. Sci. 4(1): 63–68, 3 figs., 1 table.

——— 1957. Marine algal ecology. Bot. Rev. 23: 320–350, 2 figs.

COLEMAN, J. 1933. The nature of intertidal zonation of plants and animals. Jour. Mar. Biol. Assoc. U. K. 18: 435–476, 15 figs., 7 tables.

DAWSON, E. Y. 1945. Marine algae associated with upwelling along the northwestern coast of Baja California, Mexico. Bull. South. Calif. Acad. Sci. 44(2): 57–71, pls. 20–22.

——— 1951. A further study of upwelling and associated vegetation along Pacific Baja California, Mexico. Jour. Mar. Res. 10(1): 39–58, 6 figs., 1 table.

DAWSON, G. M. 1880. Report on the Queen Charlotte Islands. Geol. Survey Can. Montreal. Pp. 1B–101B, 9 figs., 2 maps, 2 pls.

——— 1881*a*. Sketch of the geology of British Columbia. Geol. Mag. Decade 2, 8(4): 1–19, 2 figs.

——— 1881*b*. The superficial geology of British Columbia and adjacent regions. Quart. Jour. Geol. Soc. 1881 (May): 272–285, 1 fig.

——— 1888. Report on an exploration in the Yukon District, N.W.T., and adjacent northern portion of British Columbia. Can. Geol. Survey Rept. 1887: B1–B183, 7 figs., 1 map, 5 pls.

——— 1897. The Physical Geography and Geology of Canada. Handbook of Canada. Rowsell and Hutchinson, Toronto. 28 pp.

DOTY, M. S. 1946. Critical tide factors that are correlated with the vertical distribution of marine algae and other organisms along the Pacific Coast. Ecology 27: 315–328, 6 figs.

——— 1957. Rocky intertidal surfaces. In: J. W. Hedgpeth (ed.), Treatise on Marine Ecology and Paleoecology. Vol. 1, Ecology. Geol. Soc. Am. Mem. 67. Pp. 535–585, 18 figs., 2 tables.

EKMAN, S. 1935. Tiergeographie des Meeres. Leipzig. xii + 542 pp., 244 figs.

FELDMANN, J. 1937. Recherches sur la végétation marine de la Méditerranée. La Côte des Albères. Rev. Algol. 10: 1–339, 1 map, 20 pls., 25 figs., 10 tables.

——— 1951. Ecology of marine algae. In: G. M. Smith (ed.), Manual of Phycology. Chronica Botanica, Waltham. Pp. 313–334.

FISCHER-PIETTE, E. 1940. Sur quelques progrès récents, et sur les méthodes et tendances actuelles, en bionomie intercotidale (substratum rocheux, régions tempérées). Contribution à l'étude de la repartition actuelle et passée des organismes dans la zone néritique. Mém. Soc. Biogéogr. 7: 393–434.

GAIL, F. W. 1918. Some experiments with *Fucus* to determine the factors controlling its vertical distribution. Publ. Puget Sound Biol. Sta. 2: 139–151, 6 tables, 1 chart.

——— 1919. Hydrogen ion concentration and other factors affecting the distribution of *Fucus*. Publ. Puget Sound Biol. Sta. 2: 287–306, pls. 51–52, 4 tables.

——— 1922. Photosynthesis in some of the red and brown algae as related to depth and light. Publ. Puget Sound Biol. Sta. 3: 177–193, pls. 31–33, 9 tables.

GISLÉN, T. 1929. Epibioses of the Gullmar Fjord, Part I. Kristin. Zool. Sta. 1877–1927. Skr. Svensk. Vetensk. Akad. 3: 1–123.

——— 1930. Epibioses of the Gullmar Fjord, Part II. Kristin. Zool. Sta. 1877–1927. Skr. Svensk. Vetensk. Akad. 4: 1–380.

HARTOG, C. D. 1959. The epilithic algal communities occurring along the coast of the Netherlands. Wentia 1: 1–241, 27 figs., 43 tables.

HUTCHINSON, A. H. 1949. Marine plants of economic importance of the Canadian Pacific coastal waters. Proc. Seventh Pacif. Sci. Congr. 5: 62–66.

ISAAC, W. E. 1935. The distribution and zonation of marine algae on the coasts of South Africa. Brit. Assoc. Adv. Sci. Rept. Ann. Meet. 1935: 455.

LAMOUROUX, J. V. F. 1825. Distribution géographique des productions aquatiques. Hydrophytes des eaux salées. Dict. class. d'Hist. Nat. de Bory de Saint-Vincent 7: 245–251.

——— 1826. Mémoire sur la géographie des plantes marines. Ann. Sci. Nat. 7: 60–82.

OKAMURA, K. 1926. On the distribution of marine algae in Japan. Proc. Third Pacif. Sci. Congr. 1: 958–963, 1 fig.

——— 1932. On the nature of the marine algae of Japan and the origin of the Japan Sea. Bot. Mag. Tokyo 41: 588–592.

PICKARD, G. L., and D. C. MCLEOD. 1953. Seasonal variation of temperature and salinity of surface waters of the British Columbia Coast. Jour. Fish. Res. Bd. Can. 10(3): 125–145, 5 tables, 8 figs.

SCAGEL, R. F. 1948. An Investigation on Marine Plants near Hardy Bay, B. C. Prov. Dept. Fish. 1. 70 pp., 11 tables, 26 figs.

——— 1957. An Annotated List of the Marine Algae of British Columbia and Northern Washington. Bull. Nat. Mus. Can. No. 152. 286 pp., 1 fig.

SETCHELL, W. A. 1893. On the classification and geographical distribution of the Laminariaceae. Trans. Conn. Acad. Arts Sci. 9: 333–375.

——— 1917. Geographical distribution of the marine algae. Science 45: 197–204.

——— 1932. *Macrocystis* and its holdfasts. Univ. Calif. Publ. Bot. 16: 445–492, pls. 33–48.

——— 1935. Geographic elements of the marine flora of the North Pacific Ocean. Amer. Nat. 69: 560–577.

STEPHENSON, T. A., and A. STEPHENSON. 1949. The universal features of zonation between tide-marks on rocky coasts. Jour. Ecol. 37(2): 289–305, pl. 8, 4 figs.

TOKIDA, J. 1954. The marine algae of Southern Saghalien. Mem. Fac. Fish. Hokkaido Univ. 2(1): 1–264, 15 pls., 4 figs., 5 tables.

WOMERSLEY, H. B. S. 1954. The species of *Macrocystis* with special reference to those on Southern Australian coasts. Univ. Calif. Publ. Bot. 27: 109–132, pls. 1–8, 1 map.

——— 1956. The marine algae of Kangaroo Island, IV. The algal ecology of American River Inlet. Austral. Jour. Mar. Freshwater Res. 7(1): 64–87, 7 pls., 4 figs.